THERMOREGULATING ABILITY AND MINIMUM FLIGHT TEMPERATURE IN INTERIOR ALASKA DRAGONFLIES (ODONATA: ANISOPTERA)

By

Todd L. Sformo

RECOMMENDED:

Advisory Committee Chair

Chair, Department of Biology and Wildlife

APPROVED:

Dean, College of Science, Engineering and Mathematics

Dean of the Graduate School

4-21-03

Date

THERMOREGULATING ABILITY AND MINIMUM FLIGHT TEMPERATURE IN INTERIOR ALASKA DRAGONFLIES (ODONATA: ANISOPTERA)

A

THESIS

Presented to the Faculty

Of the University of Alaska Fairbanks

In Partial Fulfillment of the Requirements

For the Degree of

Master of Science

By

Todd L. Sformo, B.A., M.A., M.F.A.

Fairbanks, Alaska

May 2003

ABSTRACT

The use of operative environmental temperature (T_e) has been a major advance in the study of thermal ecology. I review the use of operative temperature in thermal biology with an emphasis on insects. Then I use data from dragonflies in Interior Alaska (Odonata: Anisoptera) to compare the efficacy of operative and ambient temperature when examining thermoregulating ability. I conclude that although the use of T_e may provide more accurate measures of thermoregulation under specific environmental conditions, the use of ambient temperature usually leads to the same conclusions about thermoregulating ability.

I next examine the relationships between thermoregulating ability, minimum flight temperature (MFT), mass, passive cooling rate, and wing loading for the ten species of dragonflies present in Interior Alaska. I investigate the influence of ambient temperature and solar radiation on daily and seasonal activity patterns. I find a range of thermoregulating abilities from complete thermoconformers to very efficient periodic thermoregulators. The ability to thermoregulate is strongly tied to body mass. Thermoconfomers have significantly lower MFTs than thermoregulators, suggesting a possible tradeoff between the ability to operate and low and high thoracic temperatures.

TABLE OF CONTENTS

List of Figures

List of Tables

ACKNOWLEDGMENTS

I gratefully acknowledge my thesis committee, especially Pat Doak. Mark Oswood was the first introduce me to the topic of dragonflies in Alaska, while Scott Armbruster introduced me to the topic of thermal biology. I was aided by discussions with Michael May, Dennis Paulson, Dave Kline, Gary Laursen, and Barbara Tudor.

I must acknowledge invaluable help from my fellow students. Luke Middle provided me with thermocouples and other instruments, Kurt Galbreath and Julie Neville (Keller) allowed me to use their vehicles, and Steve Keller provided the use of his vehicles and great conversations.

This thesis could not have been written without financial support from the University of Alaska Fairbanks, Department of Biology and Wildlife, Institute of Arctic Biology, NSF EPSCoR Graduate Fellowship, and the David Burnett Dunn Memorial Award.

I dedicate this thesis to my wife Barbara Tudor and my nieces and nephews: Carley, Colin, Emma, Erik, Justine, Renadaz, and Tatiana.

GENERAL INTRODUCTION

Thermoregulation has been defined as the elevation and maintenance of thoracic temperature in insects (Heath 1964; May 1976; Heinrich 1981). It is important to insect biology because the ability to thermoregulate has been associated with greater enzymatic efficiency in flight muscles and ultimately fitness (Heinrich 1977, 1981). To show that insects thermoregulate, one measures insect thoracic temperatures over a wide range of environmental conditions and compares these values to ambient or operative temperatures. Thermoregulators are defined by their ability to maintain a fairly constant thoracic temperature over a range of ambient conditions, while the body temperature of thermoconformers varies with ambient temperature.

A number of researchers (Heath 1964, Crawford et al. 1983, Dreisig 1984, 1990) noted that the standard procedure of comparing thoracic temperature to ambient temperature can be misleading due to the complexity of the microenvironment and its influence on an object. They propose that the comparison of thoracic temperature to operative temperature provides a more accurate measure of thermoregulating ability. Operative temperature is the temperature of a physical model such as a dead insect that is at equilibrium with the environment. Since the model is inert, it produces no heat, and its temperature is exclusively determined by the input of the environment—ambient temperature, solar radiation, substrate temperature, as well as the

major avenues of heat loss, including convection. The proposed advantage of operative temperature over ambient temperature is that operative temperature provides a species specific, integrated measurement of the environment.

I use my data on Interior Alaska dragonflies to compare measures of thermoregulatory ability with the use of ambient versus operative temperature. I find that under certain environmental conditions the operative temperature model captures the impact of declining solar radiation (S_r) while ambient temperature (T_a) lags behind in its decline. Operative temperature also displays a significant positive relationship with thoracic temperature, while T_a is significantly related to T_{th} only during particular daily periods. Operative temperature, therefore, provides a more meaningful measure than ambient temperature. Although the two measures of temperature (T_e and T_a) seldom lead to qualitatively different conclusions about thermoregulatory ability, I use operative temperature to determine thermoregulating ability because it more accurately explains species-specific thoracic temperature.

This investigation examines the thermoregulating ability and minimum flight temperatures of the adults of ten species of Interior Alaska dragonflies belonging to five genera, ranging in body mass from 0.09g to 0.86g, and fitting the two distinct behavioral types found in dragonflies (perchers and fliers). I examine how mass, passive cooling rate and wing loading are related to thermoregulating ability andminimum flight temperature (MFT). I find that smallest dragonflies have the lowest MFT and little to no ability to

thermoregulate. Medium-sized dragonflies have higher MFTs and a moderate ability to thermoregulate, while the largest dragonflies have similar MFTs but the greatest to thermoregulatory ability. One reason for these patterns is that increasing mass is associated with decreasing surface area to volume ratio and thus an increase in thoracic resistance to thermal change (thermal inertia). These differences in mass may lead to differential selection pressures on thermal strategies.

My results suggest that a tradeoff may exist between adaptation for low MFT and thermoregulating ability. Small dragonflies cannot generate or retain heat, especially during cool minimum flight conditions. They are forced to rely on the environmental inputs to reach MFT; thus it may be advantageous for them to have lower MFT to achieve flight when there is no way of warming themselves to a higher MFT. Once these small perchers reach MFT, they gain and lose heat relative to environmental conditions (thermoconformity). The advantage of thermoconformity over thermoregulation for these perchers lies in energy conservation. Thermoconformity is least expensive than thermoregulation (Corbet 1963) since thermoconformity relies only on passive heat gain and loss of thoracic temperature to changing ambient conditions.

While small species may not be capable of thermoregulating and may evolve low MFTs to compensate, the larger species thermoregulate more efficiently but may not be capable of or in need of low MFTs. These larger dragonflies are less subject to changing environmental conditions due to their

greater thermal inertia and their near universal ability to warm-up endothermically by wing-whirring (May 1976). Heat produced by wing-whiring can be effectively retained within the thorax, allowing these species to increase thoracic temperature to MFT without having lower MFT set points. My finding that MFT is independent of mass for all but the smallest species is further evidence for the claim by Vogt and Heinrich (1983) that fliers are adapted to fly at similar thoracic temperatures despite differences in climate.

Literature Cited

Convey, P. 1989. Influences on the choice between territorial and satellite behavior in male *Libellula quadrimaculata* Linn. (Odonata: Libellulidae) Behaviour 109:125-141.

Corbet, P.S. 1963. A biology of dragonflies. Quadrangle Press, Chicago.

Corbet, P.S. 1999. Dragonflies: behavior and ecology of odonata. Cornell University Press, New York.

Crawford, K.M., J.R. Spotila, and E.A. Standora. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology 64:989-999.

Dreisig, H. 1984. Control of body temperature in shuttling ectotherms. J.Thermal Biol. 9:229-233.

Dreisig, H. 1990. Thermoregulatory stilting in tiger beetles, *Cicindela hybrida* L. J. Arid Environ. 19:297-302.

Heath, J.E. 1964. Reptilian thermoregulation: evaluation of field studies. Science 146:784-85.

Heinrich, B. 1977. Why have some animals evolved to regulate a high body temperature? Am. Nat. 111: 623-640.

Heinrich, B. 1981. Ecological and evolutionary perspectives. Pages 235-302 in B. Heinrich, ed. Insect Thermoregulation. Wiley, New York.

Marden, J.H. 1995. Large sclae changes in the thermal sensitivity of flight performance during adult maturation in a dragonfly. J. Exp. Biol. 198:2095-2102.

May, M. L. 1976. Thermoregualtion and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecol. Monogr. 46:1-32.

Vogt, F.D., and B. Heinrich. 1983. Throacic temperature variation in the onset of flight in dragonflies (Odonata: Anisoptera) Physio. Zool. 56:236-241.

Chapter 1. A Literature Review on the Use and Utility of Operative Temperature in Thermal Ecology[1]

Thermal ecology is the study of the effect of temperature on the relationship between an organism and its environment. Understanding this relationship may enable one to explain range (May 1991; Corbet 1999), phenology (Norling 1971, 1984), development (Cossins and Bowler 1987), and daily activity patterns (Lutz and Pittman 1970; Michiels and Dhondt 1989; Marden et al. 1996; Coelho 2001) of many organisms. Because of the tremendous impact that temperature can have on an organism (Cossins and Bowler 1987), thermal ecology can be of interest to a diverse group biologists, from environmental physiologists to integrated pest management biologists. By studying the thermal environment of an organism, one begins to understand potential thermal constraints and may be able to predict and control insect pests (Bale 1993) or increase populations of desired game species (Forrester et al. 1998).

Early studies examining insect thermal ecology compared the temperature of living insects to ambient temperatures when trying to describe thermal effects; however, ambient temperature can change more quickly than an insect's body temperature. Furthermore, the temperature that an organism experiences (especially an insect) at a micro- and nano-climatic level may also

[1] Prepared for submission to *Odonatologica*.

differ from ambient temperature, depending on the location ambient temperature is measured (Bakken 1976; Tracey 1977). Thus, when considering the degree to which an organism controls its heat balance, one should compare the temperature of a living organism to that of an inert control with the same thermal properties as the organism in question. The temperature of a model with the same thermal properties as the study organism is referred to as effective operative environmental temperature (T_e). A dead animal, taxidermic mount, or metallic replica of similar size, shape, and color functions as the model and reacts to meteorological variables in ways very similar to a live organism but without metabolic input or behavioral repositioning. This physical model is termed effective operative environmental temperature thermometer or a T_e thermometer.

Many thermal biologists (Bakken 1976, 1992; Heinrich 1981; Dreisig 1990; May 1991; Forrester et al. 1998; Bishop and Armbruster 1999) agree that effective operative environmental temperature more accurately describes what an organism experiences thermally than ambient temperature (T_a); however, comparisons between effective operative environmental temperature and ambient temperature have not been made, especially in regard to insects. Although T_e may more accurately describe an organism's thermal experience, the question of whether or not T_e is actually more useful than T_a still remains. In this literature review, I discuss the uses of operative environmental temperature and compare the utility of it against ambient temperature by examining a subset

of my own data on dragonfly thermoregulation. I show that the use of effective operative environmental temperature rather than ambient temperature may lead to different conclusions about thermoregulating ability. These conclusions, however, differ to the degree in which dragonflies thermoregulate, and, in fact, would not have changed my general conclusions. I first present background information on the effective operative environmental temperature and a brief history of its use in animal thermoregulation. I then show how effective operative environmental temperature varies daily and/or seasonally due to changes in the relative contributions of ambient temperature, solar radiation, and their interaction on the physical models (also known as T_e thermometers). Finally, I conclude that although the use of T_e may be more appropriate during some time periods, it may not be more useful than using T_a during other periods.

Effective operative environmental temperature (henceforth "operative temperature") provides a single measure of temperature of an inert model that is at equilibrium with the environment (Bakken and Gates 1975; Bakken 1976, 1992; Crawford et al. 1983; Hertz et al. 1993; Corbet et al. 1993; Forrester et al. 1998; Bishop and Armbruster 1999). By using a T_e thermometer, the temperature of the model is due exclusively to environment effects. The model, therefore, does not contribute to heat gain or heat loss due to metabolism. By integrating the most significant environmental variables that affect an organism's body temperature including radiative, conductive, and convective

heat loss or gain, operative temperature can be used as a null model of thermoregulation with which to evaluate the potential effects of behavioral and physiological changes associated with maintaining body temperature.

The main routes of heat exchange for a body are radiation, evaporation, conduction, and convection (Cossins and Bowler 1987; May 1991; Withers 1992). Radiation can lead to both heat gain and loss. All objects above absolute zero lose heat through radiation (Withers 1992); however, this heat loss tends to be negligible in operative models and is subsumed under conduction (Church 1960). On the other hand, radiative heat gain can be significant, especially for small organisms for whom incoming solar radiation may be a primary source of heat (May 1976; Walsberg 1992). Evaporation is heat transfer *via* the change in the state of water. Previous research (Church 1960; Cossins and Bowler 1987; Bishop and Armbruster 1999) indicates that evaporative heat loss tends to be a minor component in determining insect body temperature (Casey 1992) and operative temperature (Parker 1982). Conduction, the transfer of heat between two solids, can be significant depending on amount of surface area exposed, the temperature difference between the two bodies, as well as the conductance of the two bodies (Withers 1992). For instance, some desert dwelling insects conduct heat to their bodies at certain times of the day by direct contact with warmer surfaces such as sand (Dreisig 1984, 1990). Convection, the transfer of heat between a solid and a fluid such as air (Church 1960; Withers 1992), appears to be the primary

avenue of heat transfer in operative temperature models (Church 1960; May 1991).

Due to the predominant effect of convection, operative environmental temperature has been measured in two ways. Standard operative environmental temperature (T_{es}) is an index of temperature measured under non-convective (or free convection), standardized conditions, usually in a lab setting. Operative environmental temperature (T_e) is an index of temperature measured under field conditions when convection can be variable. Unless otherwise specified, I discuss only operative environmental temperature (T_e) also referred to more simply as operative temperature.

Before the use of operative temperature models, the most common procedure for evaluating thermoregulating ability was to capture an animal and quickly record body temperature. The recorded temperature was then compared to ambient temperature. This method has two problems: a change in body temperature between capture and recording and the assumption that the instrument itself has the same heat capacity and thermal potential as the organism. Although this assumption is not valid (Winslow et al. 1937; Bakken 1980; May 1978; Crawford 1983), this method has demonstrated that insect body temperature deviates from ambient temperature and provided the first step in investigations of insect thermoregulation.

Berthold (1835) and Newport (1837) recorded both nest temperature of social insects and individual insect body temperature of bees, moths, and

beetles by pressing small thermometers against the side of resting and agitated insects. In this way, they obtained external body temperature to compare to ambient temperature and concluded that some insects ought not to be considered "cold-blooded" ectotherms because they displayed body temperatures above ambient.

Elevation of body temperature above ambient, however, is not synonymous with thermoregulation, nor does it indicate that an organism is not an ectotherm. Insect thermoregulation, like that of mammals and birds, involves temperature regulation, whereas temperature elevation can be the result of a passive physical heat gain due to a heat source, mass, volume, and other physical variables of the organism and their interaction (Heath 1964; Dreisig 1984). Thus an ectotherm may display elevated body temperature and be able to thermoregulate behaviorally, but some degree of endothermy is necessary for physiological thermoregulation. The distinction between elevation and regulation is important in the use of operative temperature (Heath 1964). Heath's (1964) primary objection to the comparison between body and ambient temperature was that no experimental control is used, and therefore body temperature elevation becomes the criterion for thermoregulation.

Heath (1964) demonstrated the problem of equating temperature elevation with thermoregulation in a simple experiment by placing cans filled with water in full sun and in shade and recording both internal can temperature and air temperature next to the can. As expected, the cans heated, cooled,

and equilibrated in relation to changing environmental conditions. Heath found that can temperature was correlated with ambient, and his results indicated that can temperature in full sun displays a similar daily pattern to that of heliothermic reptiles. When he eliminated all data below 30°C (the temperature at which reptiles begin basking), he found that can temperature could be interpreted as being independent of ambient temperature. Heath (1964) concluded that a "consistent deviation of body temperature from air temperature cannot be regarded as *prima facie* evidence of thermoregulation" because body temperature elevation can be described as a purely physical event explained by Newton's law of heat exchange (Casey 1992): an object will take on or lose heat in proportion to the difference between the object's temperature and the environment.

Heath (1964) suggested comparing body temperature to a control. While operative temperature had been used in human studies since the 1930s (Winslow et al. 1937), this was the initial call for its use in non-human physiological ecology. The use of a control provides a measure of potentially available body temperatures for comparison to live body temperatures (Heath 1964; Turner et al. 1993). To do this, one records both thoracic temperature of a living specimen and operative temperature of a model. Although Heath's first attempt (1967) at using a control was not operative temperature *per se*, he did illustrate the need for a proper operative control.

Heath (1967) captured 17-year cicadas, *Magicicada cassini*, and recorded body temperature. As a control, he recorded the temperature of tethered live cicadas in full sun. He found that as ambient temperature increased above 27°C, body temperature in the untethered specimens stopped increasing while body temperature of tethered specimens continued to increase. He related this difference directly to the thermoregulatory behavior of the untethered cicadas that moved to the underside of leaves at 27°C to decrease direct solar insolation and, therefore, body temperature. Although Heath (1967) used live tethered specimens as a control to provide evidence of potential body temperatures available to free insects, a live insect is not a true operative model.

By definition, an operative temperature model requires zero heat capacity as defined by Zeroth's law of thermodynamics (Bakken 1992): heat transfer between two thermodynamic systems proceeds from high temperature to low temperature until both are in a steady state, given each object's thermal properties. The steady state is thermal equilibrium, yet tethered live cicadas could confound the result if capable of either physiological or limited behavioral thermoregulation. A proper operative model functions as a behaviorally and physiologically inert body (Corbet et al. 1993), or a null model of thermoregulation, providing organism-specific operative temperature (Winslow et al. 1937; Crawford et al. 1983; Corbet et al. 1993) when net heat flow

between the model and environment equilibrates (Bakken 1992) and when the model has similar thermal properties to the organism in question.

While working on basking turtles *Pseudemys scripta*, Crawford et al. (1983) showed that although ambient temperature (T_a) is positively related to T_e, T_e is not equal to T_a nor does T_e have a fixed relationship to T_a. Using ten hollow metallic replicas corresponding to three size categories of turtles, they showed that T_e increases faster than T_a for all sizes at mid-day when T_a and solar radiation (S_r) reach maximum; however, during dawn and dusk, when T_a and S_r are lower, T_e approximates T_a. They also showed that T_e is more closely correlated with S_r than with T_a. The use of T_e allowed them to predict thermoregulatory basking behavior in this turtle species because T_e integrates the significant climatic conditions that in various combinations reach the minimum basking temperature (28°C). Minimum basking temperature is the temperature at which turtles of this species (*Pseudemys scripta)* begin to bask to increase body temperature by exogeneous sources. At this temperature, 98% of turtles basked. If the authors had only used ambient temperature, they would have decreased the predictive power of their model because ambient temperature did not equal minimum operative basking temperature until approximately 1130 -1200 hrs., whereas their use of operative temperature indicated that potential basking temperatures were reached from approximately 0830 - 1900 hrs.

As part of a study examining dragonfly thermoregulation (Sformo, chapter 2), I netted active, sexually mature dragonflies and recorded thoracic temperature (T_{th}) of individual dragonflies within seven seconds of capture. I also recorded temperature of a dragonfly model, ambient temperature, and solar radiation immediately after recording live-specimen temperature. The model was a specimen within the same genus, and usually the same species. The model was fully exposed to solar radiation and wind. The mean difference between operative temperature and ambient temperature increased with mass for the smallest taxa (*Sympetrum* spp., ca. 0.1 g); however, for species approximately 0.2 to 0.8 g, operative temperature remained approximately 6°C above ambient temperature. Although Crawford et al. (1983) noted that T_e increases faster than T_a for their turtle replicas, my results are not as straightforward. I found that T_e does not increase faster per unit time than T_a for all operative models (Table 1.1) which may be due to daily and/or seasonal changes in the relative contributions of ambient temperature, solar radiation, and their interaction on T_e models.

Crawford et al. (1983) concluded that the microenvironment (or nanoenvironment, see Tracy 1977; Willmer 1982; Bakken 1992) of ectotherms is too complex for a single environmental variable to be a good indicator of what an organism experiences or a predictor of potential thermoregulatory behavior because T_a, S_r, and/or substrate temperature (T_g) may interact in ways that affect ectotherm thermoregulation. In flying insects, especially, highly

complex relationships exist between height above a surface and these variables (Willmer 1982; Dreisig 1980; O'Neill and Kemp 1990, 1992).

Operative temperature has been used to determine the environmental constraints on insect body temperature and thus activity. Both Dreisig (1990) and Bishop and Armbruster (1999) measured thoracic temperatures of individual insects and operative temperatures of dead insect models in their investigations of insect thermoregulation. They regressed individual thoracic temperature on T_e, the slope of which is the thermoregulatory performance index (TPI). A slope of one indicates perfect thermoconformity while a slope of zero indicates perfect thermoregulation. Dreisig (1990) tested the hypothesis that tiger beetles (*Cicindela hybrida*) were perfect thermoregulators when engaged in stilting behavior (Dreisig 1980,1984). Stilting, the extension or straightening of legs, is thought to be a graded, thermoregulatory behavior that creates a space between body and substrate, decreasing body temperature by reducing conduction and increasing convective heat loss (Dreisig 1984). Dreisig (1984) predicted that body temperatures of tiger beetles would be constant during this activity. His results did not confirm the hypothesis of perfect thermoregulation but showed that stilting beetles are moderate thermoregulators with a TPI of 0.61. Bishop and Armbruster (1999) found a continuum of TPIs (0.96 - 0.12) among 18 species of solitary and social bees in Interior Alaska. The biophysical constraints of mass, thoracic volume, and wing loading explained both the ability to thermoregulate and to elevate thoracic

temperature above T_e at low temperatures. In general, large bees were able to thermoregulate better than small bees but required higher minimum thoracic temperatures to initiate flight after a foraging bout on flowers.

In my research on dragonflies, I too found a continuum of thermoregulating abilities related to the biophysical constraint of mass (Table 1.1, see TPI). Although in most cases my determination of whether a dragonfly is a thermoregulator or thermoconformer would not have changed, my interpretation of the degree to which a dragonfly thermoregulates would have been different if I had used ambient temperature instead of operative temperature (Table 1.1). By using T_a, I would have concluded that *Cordulia shurtleffii* was a better thermoregulator than both *Leucorrhinia* spp. and *Libellula quadrimaculata*, but the use of T_e clarifies that they are all intermediate thermoregulators of similar ability (Table 1.1). Further, the use of T_e showed that *Aeshna eremita*, the largest species, thermoregulated well; however, if I had used T_a instead, I would have concluded that it was a moderate thermoregulator comparable to species that are only 0.73 (*A. palmata*) and 0.30 (*Cordulia shurtleffii*) times as massive (Table 1.1). Thus, the use of T_e in studies of insect thermoregulation has improved our ability to detect actual behavioral and physiological thermoregulation as separate from thermal properties of an inert model. Although the extent to which an Interior Alaska dragonfly thermoregulates may be more accurately described, I did not find that

the use of T_e instead of T_a would have changed my conclusions as to whether or not a dragonfly thermoregulates.

Measuring operative temperature has also allowed researchers to verify that particular behaviors have a thermoregulatory function and to substitute operative body temperature models for actual living specimens. The method is twofold. First, body temperatures are taken from live individuals and operative models to establish the relationship between T_e and live body temperature (T_{th}). Second, operative models are heated and/or cooled (in the lab and field) and the time course of a model's heating and/or cooling (time constant) in relation to ambient temperature is recorded. Knowing the relationship between T_e and live T_{th} and the time course of a model's heating and/or cooling, researchers then substitute operative models to mimic postures, orientations, and perching heights associated with behaviors of interest to establish mean (operative) body temperatures (T_b) for different microclimate conditions and timed behaviors. The live body temperature of an organism engaged in a particular behavior for a specific time period then can be estimated based on the T_b of the specified behavior and microhabitat, the proportion of the time constant spent while engaged in the behavior, and the relationship between T_e and T_{th}.

Dreisig (1980, 1984, 1985, 1990, 1995) determined thermoregulatory behavior patterns and tested earlier models of ectotherm thermoregulation (Cowles and Bogert 1944; Heath 1964, 1965) using mean operative body temperature for the lizard *Lacerta agilis*, graylings (*Hipparchia semele*),

skippers (*Ochlodes venata*), and tiger beetles (*Cicindela hybrida*) inhabiting open sandy areas in Denmark. Dreisig (1984, 1985) used a T_e thermometer, a dead tiger beetle functioning as a hypothetical non-regulating beetle in conjunction with observations of living beetles, to show that basking time linearly decreases while foraging time increases as T_e increases until T_e reaches optimal body temperature and continuous foraging occurs. He also showed that tiger beetles increase stilting height with increasing T_e and that maximum stilting height is positively correlated to the upper beetle temperature limit before burrowing into sand to avoid lethal temperatures (Dreisig 1990). These findings would have been difficult or impossible to reach without the use of operative temperature models because body temperature of live individuals cannot be monitored continuously, and even if it could, a monitored or "wired" specimen would not be expected to exhibit normal behavior (Dreisig 1990). Also, if the "grab and stab" method had been used to find instantaneous body temperature, large number of specimens would have to be killed (Dreisig 1995). Operative temperature models, therefore, allow fewer specimens to be used, and the models can be manipulated such that body temperature and potential thermoregulating behaviors are related to a proper null model of thermoregulation.

Schultz (1998) used operative models of the tiger beetle, *Cicindel sexuttata*, to show that its life cycle and phenology are constrained by low ambient conditions. Schultz (1998) found that this deciduous woodland species

from Ohio could only maintain body temperatures within their preferred range in light gaps but not in shaded microhabitats or during the fall. Schultz (1998) speculated that these thermal constraints on body temperature may also be reflected in the unique life cycle of this species in which adults overwinter in pupal chambers, in contrast to other species within this genus that overwinter as full adults. This research demonstrates how small, inexpensive operative temperature models can be randomly deployed throughout a study site to map the thermal effects of habitat and to calculate potential thermal constraints. This method could be adapted to address questions of management such as how habitat fragmentation can impact the thermal ecology of an organism (Forrester et al. 1998) or ways in which habitats can be manipulated to thermally stress pest species.

Turner et al. (1993), like Dreisig (1980, 1985, 1990), used operative models as a proxy for live body temperatures with which to evaluate potential thermoregulatory behaviors associated with prey-capture of the burrowing spider *Seothyra henscheli* and to test theoretical alternative prey-capture tactics. On the dunes of the Namib Desert in southwestern Africa where surface temperatures can peak at 70°C (although during their research surface temperatures only reached 50°C), they used the T_e thermometer of the spider to estimate body temperature under various web locations, burrow depths, and while engaged in timed prey-capture behaviors. This research could not be done by directly measuring the body temperature of live specimens because

capture of live spiders would disturb and/or destroy the web. They predicted that particular behaviors would result in lower body temperatures so that the spider would not exceed its critical thermal maximum (CTM) of 49°C, assumed to be the spider's lethal temperature. Turner et al. (1993) showed that post-strike retreats from the web resulted in body temperatures not exceeding CMT due to the amount of time spent at depth in the burrow, but that post-retreat visits to the web do not significantly increase body temperatures because of the brief time associated with the visits. Finally, Turner et al. (1993) tested theoretical alternative prey-capture tactics to show that altered behavior would lead to potential lethal body temperature increases, and, therefore should not be considered thermal shuttling behavior. By theoretically varying time spent in particular behaviors and even eliminating some behaviors, the authors showed that that all prey-capture techniques other than the post-strike behavior resulted in spiders thermally equilibrating to environmental temperatures, which, if at CTM, could lead to spiders exceeding their lethal limit.

Seebacher et al. (1999) used a mathematical analysis of T_e to predict daily and seasonal body temperatures of large reptiles such as crocodiles, *Crocodylus porosus*. They obtained body temperatures from temperature sensitive radio transmitters sewn into chickens and fed to crocodiles. Body temperatures were obtained from eleven crocodiles of varying mass, and transmitters were retained by crocodiles from 4 to 30 days. They calculated operative temperature based on cooling constants (see also Seebacher 2000),

heat transfer from two thermally distinct layers (a skin-muscle outer layer and bone-muscle inner layer), and varying surface area exposed to ambient, substrate, and water temperature daily and seasonally. Models, in this case, are not physical but mathematical. Due to the large mass of the crocodiles, zero heat capacity cannot be assumed; therefore, they estimated operative temperature as heat transfer through the two body layers (Seebacher per. comm.). Plotting T_e for different behavioral activities and proportions of time exposed to air, ground, and water against time, Seebacher et al. (1999) showed effective daily and seasonal behavioral thermoregulation in large crocodiles weighing over 1,000 kg. While T_e varied as much as 20°C, body temperature varied only approximately 20°C. They concluded that low variability in crocodile T_bs was a function of mass and the behavioral thermoregulation technique of diurnal and seasonal shuttling between land and water microhabitats. As mass increased for crocodiles, mean T_b increased while T_b variability decreased due to decrease in the surface area to volume ratio and a concomitant increase in the width of the surface area boundary. Simultaneously, as mass increased, thermal inertia increased while convective heat loss decreased in more massive animals.

Seebacher's et al. (1999) mathematical use of operative temperature shows the further utility of operative temperature. In the absence of empirical data, they were able to use operative temperature models to extrapolate crocodile results to crocodile-like dinosaurs up to 10, 000 kg. Seebacher et al.

(1999) and Seebacher (2000) demonstrated that medium to large crocodile-like dinosaurs could also effectively thermoregulate based on biophysical principles of mass and behavioral patterns of movement between land and water.

The preceding examples illustrate the utility of operative temperature in studying thermal biology especially when organisms are inaccessible while engaged in the behaviors of interest, when measuring actual body temperature would disturb the animals in a way that would alter the results, in situations that are dangerous to both investigators and/or organisms (e.g., crocodiles), and when trying to predict thermal relations of extinct organisms such as in dinosaurs. The advantage of using of operative temperature models is that T_e thermometers more properly represent the thermal environment an organism is experiencing and is the proper null model of thermoregulation with which to evaluate the potential effects of behavioral and physiological thermoregulation. On theoretical grounds alone, it appears that operative thermometers should be used. Operative temperature thermometers have certainly allowed us to research some aspects of thermal biology that were previously extremely difficult, impossible, or would require killing large numbers of animals. There is no doubt that researchers will continue to use operative temperature as a proxy for live body temperature when access to live specimens is limited. Finally, there are other aspects of operative temperature that I have not discussed. For instance, the thermal mapping of a habitat may allow researchers to begin to

examine potential thermal constraints due to habitat fragmentation (Forrester et al.1998).

Based on my results of using T_e thermometers with Interior Alaska dragonflies, however, I do not find that operative temperature is necessarily a more robust measure of these insects's thermal equilibrium with the environment than ambient temperature. My conclusions as to which species of dragonfly thermoregulate would not have changed if I were to have used ambient temperature. The extent to which a particular dragonfly species in Interior Alaska thermoregulates may be more accurately presented when a T_e thermometer is used, but replacing the old proxy of ambient temperature may not be wholehartedly warranted at this time.

Although my results do not clearly show an advantage of using T_e thermometers over ambient temperature for these insects, there are a number of procedures that should be tested before any definitive conclusions can be reached. For instance, I did not place the T_e thermometers with respect to flier activity. By placing a number of T_e thermometers at different heights both on shore and over the water, my thermometers may have more fully captured thermal differences among these locations. Unless one is able to follow flying insects and determine activity prior to capture, these insects may have been under highly different thermal conditions than when I actually captured them. These two changes may have a greater impact than I initially suspected. I also did not orient T_e thermometers models as fully as possible for perchers. Dreisig

(1995), in contrast, used two T_e thermometers for measuring operative temperatures in "percher-like" butterflies (*Hipparachia semele* and *Ochlodes venata*). First, he mounted T_e specimens on a rotating and turning arm with which he was able to rotate through 360° as well as to tilt upward and downward. Next, he orientented T_e thermometers by mimicking the body posture, orientation, and wing position of live butterfliers and rotated the models to receive maximum and minimum solar radiation. He recorded temperature every 45°. With a second set of T_e thermometers, he repeated the above procedure except that body posture mimicked butterflies on days when the sun was not shinning and body orientation was intermediate between maximizing and minimizing incoming insolation. The combination of T_e thermometers allowed him to show that these male territorial butterflies pass through three successive behavioral phases to maximize flight efficiency but not flying time. Although my results do not show that the use of T_e provides a more in-depth understanding of dragonfly thermal biology in Interior Alaska, previous studies reviewed here demonstrate the great utility of operative temperature. More comparisons between the measures of operative and ambient temperature would allow researchers a fuller understanding of species-specific equilibrium temperatures and how these may vary due to daily and/or seasonal changes in the relative contributions of ambient temperature, solar radiation, and their interaction on T_e models.

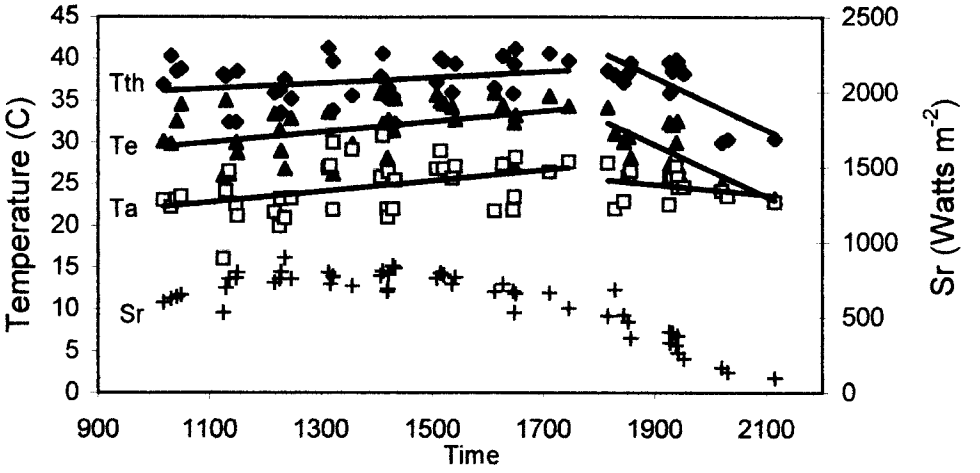

Figure 1.1. Daily changes in ambient temperature (T_a), solar radiation (S_r), the temperature of the *Cordulia shurtleffii* model (T_e), and *C. shurtleffii* thoracic temperature (T_{th}) during June 2002, near Fairbanks, Alaska. Lines represent best fit slope for piecewise linear regression. The break at 1800 hrs corresponds to the consistent decline in solar radiation in Fairbanks for June.

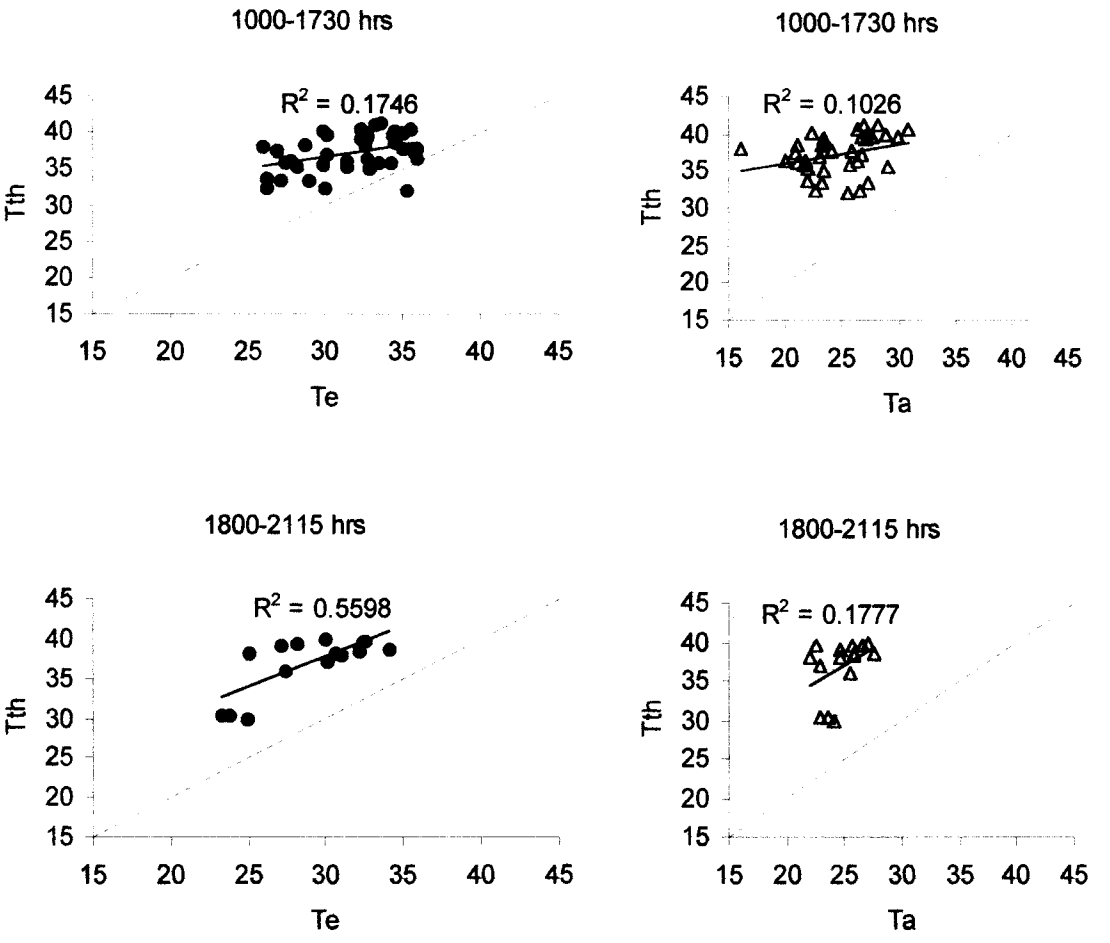

Figure 1.2. Least squares regression of *Cordulia shurtleffii* thoracic temperature on either T_e or T_a for two daily time segments.

Table 1.1. Mean mass, mean difference between operative model and ambient temperature, and slopes (TPI) of simple linear regression of operative on ambient temperature, thoracic on operative temperature, and thoracic on ambient temperature by species for eight species of dragonflies collected and tested near Fairbanks, Alaska between June and August 2001 and 2002.

Taxon	Mean (±SE) body mass (g) [N]	Mean (±SE) difference (Te - Ta) [N]	Slope (Te on Ta) (R^2) [N]	TPI = Slope (Tth on Te) [N]	Slope (Tth on Ta) [N]
Sympetrum internum	0.09 (0.002) [55]	3.88 (0.64) * [19]	0.8 (0.19) [38]	0.96[a] [38]	1.07[a] [38]
Sympetrum danae	0.10 (0.002) [139]	4.84 (0.55) * [43]	0.69 (0.35) [82]	0.98[a] [82]	0.99[a] [82]
Leucorrhinia spp	0.22 (0.005) [106]	6.23 (0.45) * [37]	1.13 (0.52) [73]	0.4 [73]	0.59 [73]
Cordulia shurtleffii	0.27 (0.005) [43]	6.00 (0.69) * [27]	0.54 (0.16) [55]	0.46 [55]	0.37 [55]
Libellula quadrimaculata	0.40 (0.007) [85]	6.19 (0.71) * [20]	1.11 (0.44) [44]	0.47 [44]	0.55 [44]
Aeshna palmata	0.64 (0.004) [149]	6.23 (0.73) * [16]	1.3 (0.50) [30]	0.19[b] [30]	0.28[b] [30]
Aeshna interrupta	0.65 (0.004) [106]	6.13 (0.55) * [34]	1.54 (0.73) [66]	0.06[b] [58]	0.14[b] [66]
Aeshna eremita	0.89 (0.006) [47]	5.89 (0.78) * [19]	0.98 (0.55) [36]	0.17[b] [36]	0.34 [36]

* Significant difference at $P < 0.001$, Wilcoxon Matched-Pairs of T_e and T_a.
[a] slope = 1, $P > 0.05$, thermoconformer.
[b] slope = 0, $P > 0.05$,- thermoregulator.

Table 1.2. Results of multiple regression models examining the impact of ambient temperature (T_a) and solar radiation (S_r) on the operative environmental temperature of a *Cordulia shurtleffii* model during two daily time ranges.

Period	Parameter	t	P
1000-1745 hrs (n = 38)	T_a	2.09	0.04
	Sr	-0.13	0.90
	T_a^2	-1.87	0.70
	Sr^2	0.06	0.95
1800-2115 hrs (n = 15)	T_a	-1.67	0.13
	Sr	3.58	0.01
	T_a^2	1.69	0.12
	Sr^2	-2.52	0.03

Literature Cited

Bakken, G.S. 1976. A heat transfer analysis of animals: unifying concepts and the applications of metabolism chamber data to field ecology. J. Theor. Bio. 60: 337-384.

--. 1980. The use of standard operative temperature in the study of the thermal energetics of birds. Physio. Zool. 53: 108-119.

--. 1992. Measurement and application of operative and standard operative temperatures in ecology. Am. Zool. 32:194-216.

Bakken, G.S., Gates, D.M. 1975. Heat-transfer analysis in animals: some implications for field ecology, physiology, and evolution. Pages 255-90 in DM Gates and RB Schmerl, eds. Perspectives of Biophysical Ecology. Berlin: Springer.

Bale, J., S.R. Leather, and K.F.A Walters. 1993. The Ecology of Insect Overwintering. Cambridge University Press, Cambridge.

Berthold, A.A. 1835. Neue Versuche uber die Temperatur der kaltblutigen Thiere. In der Dieterischen Buchhandlung, Gottingen.

Bishop, J.A., and Armbruster, W.S. 1999. Thermoregulatory ability of Alaskan bees: effects of size, phylogeny and ecology. Funct. Ecol. 13:711-24.

Casey, T.M. 1992. Biophysical ecology and heat-exchange in insects. Am. Zool. 32:225-237.

Church, N.S. 1959. Heat loss and the body temperatures of flying insects II. Heat conduction within the body and its loss by radiation and convection. J. Exp. Bio. 37:186-212.

Coelho JR 2001 Behavioral and physiological thermoregulation in male cicada killer (*Sphecius speciosus*) during territorial behavior. Journal of Thermal Biology 26: 109-116

Corbet, P.S. 1999. Dragonflies: behavior and ecology of odonata. Cornell University Press, New York.

Corbet, S.A., M. Fussell, R. Ake, A. Fraser, C. Gunson, A. Savage, and K. Smith. 1993. Temperature and the pollinating activities of social insects. Ecol. Entom. 18:17-30.

Cossins, A.R., and K. Bowler. 1987. Temperature Biology of Animals Chapman and Hall: New York.

Cowles, R.B., and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Am. Mus. Nat. Hist. 83:265-296.

Crawford, K.M., J.R. Spotila, and E.A. Standora. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology 64:989-999.

Dreisig, H. 1980. Daily activity, thermoregulation, and water loss in the tiger beetle *Cicindela hybrida*. Oecologia 44:376-89.

--. 1984. Control of body temperature in shuttling ectotherms. J.Thermal Biol. 9:229-233.

--. 1985. A time budget model of thermoregulation in shuttling ectotherms. J. Arid Environ. 8:191-205.

--. 1990. Thermoregulatory stilting in tiger beetles, *Cicindela hybrida* L. J. Arid Environ. 19:297-302.

--. 1995. Thermoregulation and flight activity in territorial male graylings, *Hipparchia semele* (Satyridae), and large skippers, *Ochlodes venata* (Hesperiidae). Oecologia 161:169-176.

Forrester, N.D., F. Guthery, S.D. Kopp, and W.E. Cohen. 1998. Operative temperature reduces habitat space for Northern Bobwhites. J. Wild Manage. 62:1506-11.

Heath, J.E. 1964. Reptilian thermoregulation: evaluation of field studies. Science 146:784-85.

Heath, J.E. 1967. Temperature responses of the "17-year" cicada, *Magicicada cassinii.* Am. Midland Natural. 77:64-76.

Heath, J.E., and P.A. Adams. 1965. Temperature regulation in the sphinx moth during flight. Nature 205:309-310.

Heinrich, B. 1974. Thermoregulation in endothermic insects. Science 185:747-756.

--. 1977. Why have some animals evolved to regulate a high body temperature. Am. Nat. 111: 623-640.

--. 1981. Ecological and evolutionary perspectives. Pages 235-302 in B. Heinrich, ed. Insect Thermoregulation. Wiley, New York.

Hertz, P.E., R.B. Huey, and R.D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am. Nat. 142:796-818.

Lutz, P.E., and A.R. Pittman. 1970. Some ecological factors influencing a community of adult odonata. Ecology 51:279-285.

Marden, J.H. M.G. Kramer, and J.H Frisch. 1996. Age-related variation in body temperature, thermoregulation and activity in a thermally polymorphic dragonfly. J. Exper. Biol. 199:529-535.

May, M. L. 1976. Thermoregualtion and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecol. Monogr. 46:1-32.

--. 1978. Thermal adaptations of dragonflies. Odonatologica 7:27-47.

--. 1991. Thermal adaptations of dragonflies, revisited. Advan. Odonatology 5:71-88.

Michiels, N.K, and A.A. Dhondt. 1987. Coexistence of three *Sympetrum* species at Den Diel, Mol, Belgium (Anisoptera: Libellulidae) Odonatologica 16: 347-360.

Newport, G. 1837. On the temperature of insects, and its connection with the functions of respiration and circulation in the class of invertebrated animals Philosophical Transactions of the Royal Society, London 127: 259-339.

O'Neill K.M., and W.P. Kemp. 1990. Behavioral responses of the Robber Fly *Stenopogon inquinatus* (Diptera: Asilidae) to variation in the thermal environment. Environ. Entom. 19:459-464.

O'Neill K.M., and W.P. Kemp. 1992. Behavioral thermoregulation in two species of robber flies occupying different grassland microhabitats. J. Thermal Biol. 17:323-331.

Parker, M.A. 1982. Thermoregulation by diurnal movement in the barberpole grasshopper (*Dactylotum bicolor*). Am. Midl. Nat. 107: 228-237.

Schultz, T.D. 1998. The utilization of patchy thermal microhabitats by the ectothermic insect predator, *Cicindela sexguttata*. Ecol. Entom. 23:444-450.

Seebacher, F., G.C. Grigg, and L.A. Beard. 1999. Crocodiles as dinosaurs: behavioral thermoregulation in very large ectotherms leads to high and stable body temperatures. J. Exp. Biol. 202:77-86.

Seebacher, F. 2000. Heat transfer in a microvascular network: the effect of heart rate on heating and cooling in reptiles (*Pogona barbata* and *Varanus varius*). J. Theor. Biol. 203:97-109.

Tracy, C.R. 1977. Minimum size of mammalian homeotherms: role of the thermal environments. Science 198:1034-35.

Turner, J., J.R. Henschel, and Y.D Lubin. 1993. Thermal constraints on prey-capture behavior of a burrowing spider in a hot environment. Behav. Eco. Sociobiology 33:35-43.

Wendler, G., and F. Eaton. 1983. Solar radiation data for Fairbanks. Geophysical Institute, University of Alaska Fairbanks.

Willmer, P.G. 1982. Microclimate and the environmental physiology of insects. Pages 1-57in M.J. Berridge, J.E. Treherne, and V.B. Wigglesworth eds. Advances in Insects Physiology, Vol. 16. Academic Press, London.

Winslow, C.E.A, L.P Herrington, and A.P Gagge. 1937. Physiological reactions of the human body to varying environmental temperatures. Amer. J. Physio. 120:1-22.

Chapter 2. THERMOREGULATING ABILITY AND MINIMUM FLIGHT TEMPERATURES IN DRAGONFLIES (ODONATA: ANISOPTERA) FROM INTERIOR ALASKA[2]

INTRODUCTION

The ability of insects to thermoregulate has been shown in a number of studies (Heath and Adams 1965; Heinrich 1974. See May 1976 and Heinrich 1981 for reviews). For many insects the ability to both elevate and regulate body temperature is positively correlated with the intensity and duration of activities that directly influence fitness (Heinrich 1977, 1981; Singer 1987; Convey 1989; Ybarrondo and Heinrich 1996). However, there is not a single variable or suite of variables that allow researchers to specify *a priori* whether an insect should be able to thermoregulate. Rather, what is found is a continuum of abilities, ranging from a high degree of thermoregulation to none at all (thermoconformity).

One reason for this continuum of abilities is the variable extent to which insects can utilize different thermoregulatory mechanisms. Subtle changes in behavior such as orientation toward a heat source and microhabitat selection, as well as the physiological ability to shunt hemolymph to dissipate or increase thoracic temperature, have allowed a variety of insects to exploit a wide range

[2] Prepared for submission to *Physiological Zoology*

of habitats (May 1976, 1991; Bishop and Armbruster 1999). This suggested that the ability to operate at high thoracic temperatures could be advantageous to fitness regardless of geographic location. However, insects that typically encounter cool ambient temperatures may benefit from an ability to be active at low thoracic temperatures (Sailor 1950; Heinrich and Mommsen 1985), and in some cases being able to commence activity at low body temperature may be a more favorable strategy than elevating body temperature.

The purpose of the present study is to examine the strategies used by adult dragonflies (Odonata: Anisoptera) in Interior Alaska to commence and continue adult activities throughout the day. I concentrate on the thermoregulating ability and minimum flight temperature of these species. Adult dragonflies are ideal subjects due to their cosmopolitan distribution (Corbet 1963; 1999; May 1991), wide range of mass (May 1976; Grabow and Ruppell 1995), and conspicuous thermoregulatory behaviors (Corbet 1963; 1999; May 1976, 1978, 1991; Heinrich and Casey 1978). The ability of adult dragonflies to both thermoregulate and fly at low thoracic temperatures is positively correlated with mass and predominate behavior at ponds (May 1976; Heinrich and Casey 1978; Vogt and Heinrich 1983). Smaller dragonflies tend to be ectothermic perchers and typically employ behavioral thermoregulation, whereas larger species tend to be periodically endothermic fliers that employ a combination of behavioral and physiological thermoregulation to control body temperature (Corbet 1963, 1999; May 1976, 1978, 1998; Parr 1983; Vogt and Heinrich

1983; Heinrich 1981, 1991). Heinrich and Casey (1978) noted that the superior thermoregulating ability of fliers may be due to their ability to shunt hemolymph, while perchers must rely on behavioral changes.

To initiate flight or regulate body temperature, insect flight muscles can reach a minimum temperature by one of three means: 1) insects remain at rest until ambient temperature increases flight muscle temperature to minimum flight temperature (MFT), 2) insects behaviorally position themselves to receive the maximum exogenous inputs to heat muscles to MFT (May 1976, 1978; Vogt and Heinrich 1983; Heinrich 1991), or 3) insects physiologically augment exogenous environmental inputs by endogenous warm-up to reach MFT (May 1976, 1978, 1998; Vogt and Heinrich 1983; Heinrich 1991). Species incapable of endogeneous heat production may benefit from having a lower MFT which expands their activity period. However, species capable of endogenous heat-production may be able to reach MFT without having low MFT set points, and they may benefit most by maximizing activity through maintenance of high thoracic temperature. Thus two distinct strategies for maximizing adult activity may exist. Heinrich (1977) further suggested that specialization at both high or low thoracic temperature may be incompatible because insects adapted to fly at low thoracic temperatures may be unable to operate at high thoracic temperatures and vice versa. This specialization suggests a possible tradeoff between MFT and thermoregulating ability.

In this paper, I investigate evidence for a possible tradeoff between thermoregulating ability and minimum flight temperature. First, I determine thermoregulating ability and minimum flight temperature for a suite of species. Then I examine relationships between thermoregulating ability and mass, passive cooling rate, and wing loading. Next, I relate seasonal and daily activity patterns to the thermal input of both ambient temperature and solar radiation to show the extent of dependence of dragonfly activity upon these abiotic factors. Finally, I compare my results to previous lower-latitude studies (May 1976; Vogt and Heinrich 1983; Polcyn 1994) to address whether differences in thermal physiology exist between high- and low-latitude species.

METHODS

The dragonfly (Anisoptera) community of Interior Alaska near Fairbanks (64°48'N; 147°42'W) consists of ten species in five genera (Table 2.1). Three of the genera contain perchers and the other two contain fliers (pers. obs.). In this study, I consider species individually (unless otherwise noted) in all cases except for the three *Leucorrhinia* spp., which I could not identify to species in the field.

Mean fresh total body mass for adults varies nine-fold among species from the lightest *Sympetrum internum* (0.09g) to the heavier *Aeshna eremita* (0.86g) (Table 2.1), and mass significantly differs among taxa with the exception of the species pairs *Aeshna interrupta* and *A. palmata* and *Sympetrum danae* and *S. internum* (Table 2.1). Mean thoracic mass varies

eight-fold between the taxa and displays a similar pattern to that of total body mass (Table 2.1).

All field work was conducted at three ponds near Fairbanks, Alaska: an artificial pond behind the small airplane runway at the Fairbanks International Airport; Sheep Creek pond located on the east side of Sheep Creek Road at the junction with Gold Hill Road; and a pond located north of Ballaine road approximately one-half kilometer east of Goldstream Creek. The pond at the Fairbanks International Airport, subsequently razed in spring 2002, was a fishless pond approximately 1364 meters long with a maximum width of 40.5 meters covering up to 30,000m^2. The Sheep Creek pond is also fishless and covers approximately 1019.5m^2, while the Ballaine road pond is part of a large wetland area associated with Goldstream creek and had only one measurable shore approximately 30 meters in length.

The summertime thermal environment of Interior Alaska differs from that of lower latitudes by having significantly lower average daily temperatures compared to sites in Maine, New Jersey and Florida (Wilcoxon Rank Sums, $P < 0.0001$; Fig. 2.1). Dragonflies in Interior Alaska also experience a shorter season available for activity and longer day length (Figs. 2.1 and 2.2).

Cooling Curves

To measure cooling curves for Fairbanks species, a cooper/constantan thermocouple lead was implanted into the thorax of a freshly killed individual which was mounted four centimeters above a Styrofoam block. The

mounted dragonfly was heated with a 250 watt infrared heat lamp until thoracic temperature (T_{th}) was 22 °C above ambient. The lamp was then turned off and thoracic temperature was recorded every five seconds as the individual cooled. Standard operative environmental temperature (T_{es}: the temperature of a dead, mounted dragonfly of the same species, placed approximately one meter from the heating source in still air) was recorded approximately every five seconds as the freshly killed individual cooled. Cooling curves (thoracic temperature vs. time) were generated for each species and showed approximately exponential decay, as expected. The difference between T_{th} and T_{es} was calculated and then log-transformed to obtain a linear relationship with time. The slope of the log-linearized relationship is the passive cooling rate K (°C/min). I used ANCOVA to examine the influence of mass, taxon, and their interaction on passive cooling rate. I then performed all pairwise comparisons between species using a Tukey-Kramer procedure for multiple comparisons. To ensure model assumptions were met for this and all other analyses, I visually examined scatterplots for deviations from normality.

Wing Loading

To determine wing area and wing loading for each species, I clipped fore- and hind- wings at the base of the four main veins distal to the wing joint. The wings, a ruler, and a one-square centimeter piece of paper were color-photo scanned at 150 dots per inch. Using NIH Image software (Scion Image™), I standardize length and area and traced wing perimeter. Wing

loading was determined as a ratio of fresh mass (g) to wing area (cm^2). I examined the influence of mass, taxon, and their interaction on wing loading by performing ANCOVA. I then performed all pairwise comparisons between species using a Tukey-Kramer procedure for multiple comparisons.

Minimum Flight Temperature

From May to mid-September in 2000 and 2001, I measured minimum flight temperature (MFT); measurements were taken in the lab, at the Institute of Arctic Biology Greenhouse, or at the nearby study ponds.

To estimate MFTs, I recorded the lowest temperature at which a species maintained level flight (following methods of May 1976, 1978, 1998). For field measurements, I located roosting individuals unable to fly during cool mornings. Once I determined that individuals could not fly, I heated them in my hands, released and then recaptured them after a horizontal flight of a few meters. Upon recapture, I recorded thoracic temperature (T_{th}) with a thermocouple thrust into the thorax. Since it is not always possible to locate roosting individuals of all species in the field, I brought specimens of some species into the lab and cooled them in a refrigerator. To estimate MFT, I warmed specimens and tossed them into the air. Once they were able to maintain horizontal flight by flying to a mesh net a few meters away, I recorded T_{th} as above. I examined the influence of mass and taxa on MFT by performing ANCOVA.

To examine whether Alaskan individuals have lower MFTs than those from lower latitudes, I used two sided *t*-tests to compare the estimated MFTs from my research to those of species from other regions (May 1976, 1979, 1991, 1998; Vogt and Heinrich 1983). I based comparisons on similarity in total body mass and behavior as well as recommendations from M. May (per. comm.) and B. Heinrich (pers. comm.)

Thermoregulation

To measure thermoregulating ability, I netted active, sexually mature dragonflies at each study site between 0500 to 2400 hrs Alaska Daylight Time (ADT) throughout a species' flight season. I recorded T_{th} of individual dragonflies within seven seconds of capture using a thermocouple (Physitemp BAT 12) equipped with a 29-gauge copper-constantan (Cu-Cn) probe. The lead was thrust into the thorax ventrally and posterior to the last pair of legs. If the interval between capture and acquisition of thoracic temperature exceeded seven seconds, the dragonfly was collected but only used for morphometric analysis. I also recorded temperature of a dragonfly model immediately after recording live-specimen temperature. The model was a freshly killed specimen within the same genus, and usually the same species, placed in an unshaded location and at equilibrium temperature with the environment, given the model's particular thermal properties of size, shape, and color (Crawford et al. 1983; Hertz et al. 1993; Forrester et al. 1998). The model's thoracic temperature was used as an estimate of operative

environmental temperature (T_e). After recording live and model temperature, I used the same thermocouple to measure ambient temperature (T_a), and I measured solar radiation with a Li-Cor photometer placed horizontally on a foam pad at ground level and free from any obstruction.

I transported live specimens in partially sealed, labeled plastic bags in a cooler with moistened towels to prevent desiccation. Total body mass was usually measured within five hours, and thoracic and abdominal mass, total body length, forewing and hindwing length were measured within 24 hours.

For each species, the Thermoregulatory Performance Index (TPI) was computed as the slope of the regression line of T_{th} against T_e (Bishop and Armbruster 1999). To determine if species thermoregulate, I compared TPI to a theoretical isothermal line (slope = 1) that represents perfect thermal conformity, as well as a slope = 0 which represents perfect thermoregulation.

The thoracic temperature that I measured for perchers during perching activity may be somewhat inflated. It is difficult to net individuals without eliciting take-off and hovering. Although I did not record thoracic temperatures of individuals that hovered for more than two seconds before capture, inevitable thoracic heating is likely even for as short a period of flight as two seconds and may contribute to increased thoracic temperature. However, it is unlikely that this error is great enough to affect TPI indices since the temperature is raised

consistently only 1-2 °C (pers. obs.) regardless of T_{th}, resulting in a slighty elevated but parallel slope of the regression line of T_{th} against T_e.

Phenology and Activity Patterns

In 2001, I examined adult phenology and surveyed hourly activity whenever I was in the field collecting thermoregulation data. From June 7-September 15, 2001, I surveyed study ponds a total of 26 times for a total of 220 hours over the season. At least once each month, I examined activity at the Sheep Creek Pond continuously from 0600-2400 hrs in order to determine times of first and last daily activity. I set up twelve eight-meter^2 quadrats at each of the three study ponds. The quadrats were two meters wide and extended two meters over the pond and two meters on shore. Each hour, I surveyed activity by counting and categorizing individuals (genus and/or species) that either perched in or flew through the quadrats. Quadrats were surveyed for 30 seconds at a time. Dragonfly activity for a given time period was calculated as the mean number per quadrat averaged over all 12 quadrats.

I used linear mixed models to examine the factors impacting activity levels for the different genera. I examined the effects of date, time of day, ambient temperature, solar radiation, and all two-way interactions. For time of day, I included a pre- and post- active period. Ambient temperature and solar radiation were calculated as the mean of measurements taken just prior to and immediately after each hourly survey; both their linear and quadratic effects were examined in the models. Study site was included as a random effect.

Nonsignificant interactions were dropped from models. To ensure model assumptions were met, I visually examined scatterplots. The reported results are for the reduced models.

RESULTS

Cooling Curves

Across species, the passive rate of cooling declined with increasing mass ($F_{1,36}$ = 8.46, P = 0.0065; Fig. 2.3), indicating that smaller dragonflies cool more rapidly than larger dragonflies. Neither species ($F_{1,36}$ = 0.35, P < 0.5590) nor the mass by species interaction ($F_{1,36}$ = 0.99, P < 0.3280) were significant. However, the rate of passive cooling was significantly higher in the *Sympetrum* spp. and *Leucorrhinia* spp. than all larger species (Fig. 2.3).

Wing Loading

Wing loading increased with mass across taxa ($F_{1,70}$ = 151.86, P < 0.0001; Fig. 2.4) and varied significantly among species ($F_{7,70}$ = 5.92, P = 0.01). The interaction between species and mass was also significant ($F_{1,70}$ = 5.14, P = 0.02), but for all taxa there was either a positive relationship between wing loading and mass or no significant change over the small range of mass measured for each species. Pairwise comparisons indicated that wing loading increases with mass to a certain extent regardless of percher-flier status and begins to level off at 0.2 g, although the aeshnids are significantly greater than all other species.

Minimum Flight Temperature (MFT) of Dragonflies in Interior Alaska

When all species were considered, MFT significantly increased with mass ($F_{1, 68} = 35.34$, $P < 0.0001$; Fig. 2.5) and varied significantly among species ($F_{7, 68} = 4.44 = 2.11$, $P = 0.03$); however, the interaction was not significant. Least square means with Tukey-Kramer procedure for multiple comparisons indicated that while larger perchers display higher MFTs than smaller perchers, MFTs do not significantly differ between the various fliers (Fig. 2.5). Even the most and least massive fliers (*Aeshna eremita* and *Cordulia shurtleffii*), which differ threefold in mass, did not differ in MFT (Fig. 2.5).

MFT Comparisons among Latitudes

I obtained comparable MFT data for percher species from Maine (Vogt and Heinrich 1983, 44°N), New Jersey (May 1998, 42°N), and Florida (May 1976, 28°N); however, comparable data for fliers were obtained only from Florida (May 1976). When I examined whether Interior Alaska perchers had lower MFTs than comparable species from lower latitudes, I found varied results. MFTs of *Sympetrum* spp. in Interior Alaska were slightly but significantly greater than *Sympetrum vicinium* and *S. obtrusum* in Maine (44°N, Table 2.2); however, Alaskan *Sympetrum* spp. had lower MFTs than *Sympetrum vicinium* in New Jersey (42°N, Table 2.2). *Leucorrhinia* spp. had significantly lower MFTs than *Pachydiplax longipennis* and *Erythemis*

simplicicollis in Florida, and MFT of *Libellula quadrimaculata* was slightly but significantly greater than *Libellula* spp. in Florida (Table 2.2).

The only available study that examined MFT for fliers at lower latitudes is May (1976), and he found that in general MFT for species of sizes comparable to Alaskan species (from approximately 0.3g to 0.6g) only ranged between 20-23°C. Of the five comparisons I examined, in two cases the Alaskan species had significantly higher MFT and in the other three cases there was no significant difference in MFT (Table 2.2).

Thermoregulation

Perchers

Not all perchers thermoregulate. Both *Sympetrum* species appeared to be thermo-conformers; their thermoregulatory performance indices did not differ significantly from the isothermal line (Table 2.1, Fig. 2.6). In contrast, TPI for *Leucorrhinia* spp. and *Libellula quadrimaculata* indicated moderate thermoregulatory abilities (Table 2.1, Fig. 2.6).

Fliers

On the other hand, all fliers thermoregulated. The smallest flier *Cordulia shurtleffii* had an intermediate TPI that is similar to that of the larger percher species; thus, it has a moderate ability to thermoregulate. In contrast, all three aeshnid species had TPIs not significantly different from zero, indicating that they are very good thermoregulators (Table 2.1, Fig. 2.6).

Phenology and Activity Patterns

In 2000-2001, adult dragonfly activity in Interior Alaska began in late May-early June and continued through mid-September; this matches a general pattern reported by Paulson (1999). Unless otherwise noted, activity results are from 2001. The highest species richness was observed from early June through mid July. Within four days of observing first adult activity, both perchers and fliers were active and up to five species (*Leucorrhinia borealis*, *L. proxima*, *L. glacialis*, *Libellula quadrimaculata*, and *Cordulia shurtleffii*) co-occurred at ponds on a majority of days during the period June 9 to July 21, 2001 (Fig. 2.7).

The activity of *Libellua quadrimaculata* and *Cordulia shurtleffii* dropped off by late-June to early-July, 2001, while *Leucorrhinia* spp. continued until July 21. Within this initial activity period, the genus *Aeshna* appeared on June 23. The addition of aeshnids (*Aeshna eremita, A. palmata,* and *A. interrupta*) marked maximum species richness of eight co-occurring fliers and perchers.

During the period July 22 through August 4, 2001, only the three *Aeshna* species were observed. The perchers in the genus *Sympetrum* (*Sympetrum danae* and *S. internum*) appeared on August 6, alongside *Aeshna* fliers, and both genera continued activity through September 15, 2001, when I ended my observations (Fig. 2.7).

I do not have survey data for *Sympetrum internum* because they were seldom present at ponds in either years. They appeared to spend most of their

time in fields where they forage, copulate, and oviposit on moist soil or at small ephemeral ponds.

Perchers

All perchers showed a pattern of increasing activity with increasing T_a (Table 2.3), and all showed a significant response to the quadratic effect of time of day (Table 2.3, Fig. 2.8). *S. danae* displayed a significant negative response to S_r, as well as a number of significant interactions (Table 2.3, Fig. 2.8).

Fliers

Cordulia shurtleffii activity significantly decreased with T_a; the linear and quadratic effects of time of day were also significant, but the effect of S_r was not significant (Table 2.3, Fig 2.8).

The *Aeshna* spp. displayed a strikingly different pattern than all other taxa. They were active from early morning (0800hrs) to late evening (2400hrs) (Fig. 2.8), and displayed no significant relationships between activity and any of the tested effects (Table 2.3).

DISCUSSION

Perchers

Interior Alaska Anisoptera follow the general pattern in which smaller dragonflies show percher behavior, short duration sallies between extended periods in horizontal perched position (Corbet 1963, 1999; May 1976, 1978, 1991; Grabow and Ruppell 1995). Despite the similarity in behavior among the three-percher genera, their four-fold variation in mass is associated with large

differences in MFT and thermoregulation. Lower mass decreases thermal inertia, allowing heat to be both gained and lost at a faster rate than in larger species (May 1976; Bartholomew 1981; Vogt and Heinrich 1983; Casey 1992; Bishop and Armbruster 1999). Because perchers tend to be of low mass and ectothermic, and because I have not witnessed any percher wing-whirring either in the lab or field, perchers are potentially more influenced by environmental conditions than larger species with greater thermal inertia.

For body mass below approximately 0.2 g, I found that the rate of passive cooling rises quickly (Fig. 2.3), indicating a poor ability to retain heat. The smallest perchers, *Sympetrum* spp., are strictly ectothermic and thermoconforming (Table 2.1), so that their behavior is determined by heat input from the environment. These perchers are able to reposition themselves to elevate body temperature but can only attain an approximately 2.2 °C temperature elevation regardless of ambient temperature. In contrast, the larger *Leucorrhinia* spp. and *Libellula quadrimaculata* are ectothermic but capable of thermoregulating (Table 2.1). These perchers are able to both elevate and maintain a fairly constant body temperature over a wide range of ambient temperatures by changes in position, orientation, and posture. Consequently, their activity is less tied to environmental conditions than that of the smaller perchers.

Perchers are known to engage in both heat-gaining and heat-reducing behaviors (Corbet 1962, 1999; May 1976, 1978, 1987, 1991). In the field, I

observed heat-gaining behavior nearly every time *Sympetrum* spp. and *Leucorrhinia* spp. landed. Individuals perched so as to intercept solar radiation in two ways. First, they pointed the long axis of their bodies perpendicular to the incoming solar radiation, and, second, they oriented their already spread-wings downward and foreword. Wings are thought to trap heat either by forming a "micro-greenhouse" that confines long wave radiation from incoming solar radiation around its thorax (Corbet 1999) and/or by intercepting heat radiating from an underlying substrate such as the ground or reflective stones (May 1976; Corbet 1999). The use of these postures and wing orientations has been described as heat-gaining in dragonflies (May 1976, 1998; Tracey et al. 1979) and moths and butterflies (Kingsolver 1983, 1985, 1987). In contrast, I observed *Sympetrum danae* and *Leucorrhinia* spp. in the heat-reducing obelisk position (i.e., wings depressed, head and thorax tipped forward and away from incoming solar radiation, abdomen pointed upwards) only in the lab at temperatures of approximately 35-37 °C, and not when perched at ponds. Some dragonfly species use the obelisk behavior to slow heat gain by shading the thorax and decreasing the surface area exposed to solar radiation (Corbet 1963, 1999; May 1976, 1991). My observations, therefore, suggest that the challenge for these species is gaining and retaining enough heat for activity rather than dissipating heat.

In contrast to the smaller perchers, *Libellula quadrimaculata* engaged in both heat-limiting and heat-gaining behavior, with the second behavior being

more frequent (pers. obs.). Although *Libellula quadrimaculata* did not use the obelisk behavior in the lab or field, I did observe that they would perch vertically on vegetation, appearing to use a stem to shade the thorax. Thus, the largest Interior percher used heat-limiting activity.

Wings can contribute to the maintenance of favorable thoracic temperature in a second way. Wing loading measures the amount of effort a dragonfly must expend to remain aloft. Generally, wing loading increases with mass (Bartholomew and Heinrich 1973), and all Interior Alaska perchers have low wing loading (Fig. 2.4), indicating that they require relatively little power to remain aloft during flapping flight. While this indicates that compared to many species, they generate little heat while in-flight, it may still be a significant input to their overall heat load (Bartholomew and Heinrich 1973). Given the general positive relationship between wing loading and mass in dragonflies (Bartholomew and Heinrich 1973), *Leucorrhinia* spp. may have slightly higher than expected wing loading while *Libellula quadrimaculata* has a lower than expected wing-loading for species of their respective masses. The wing loading in *Leucorrhinia* spp. indicates a trend toward a higher level. With a higher level, *Leucorrhinia* spp. may generate more heat, potentially contributing to greater thoracic elevation than *Sympetrum* spp. The lower than expected wing loading in *Libellula quadrimaculata* may allow *Libellula quadrimaculata* to decrease excessive thoracic heat by forced convective heat loss, as May (1976, 1991, 1995) has reported for flier species. Although *Libellula*

quadrimaculata is a percher and not a flier, my observations indicate that it flies much more often and for longer periods than any other Interior Alaska percher.

Although I was surprised at the moderate thermoregulating ability of *Leucorrhinia* spp. and *Libellula quadrimaculata*, perchers can display a range of thermoregulating abilities. May (1976, 1998) showed that, despite their small size, some perchers are able to thermoregulate well by postural adjustments alone. For instance, Ishizawa (1991, 1994, 1998, as reported by May 1998) has shown variability in thermoregulating ability among other species in the genus *Sympetrum*, with some thermoregulating well (TPI = 0.1, based on a regression of T_{th} on T_a) while others are complete thermoconformers (TPI = 0.9). May (1998) also showed that *S. vicinum* (0.1 g) orient their body and wings similarly to Interior Alaska *Sympetrum* spp. and *Leucorrhinia* spp. (pers. obs.) and are able to thermoregulate as well as, and sometimes better than (slope of T_{th} on T_a is 0.31 for *S. vicinum*) *Leucorrhinia* spp. The variation in *Sympetrum* thermoregulatory ability among studies may be due to differences in ambient temperature between regions (Fig. 2.1). Even endothermic warm-up, an activity more typical of larger species, has been reported in very small dragonfly species (May 1976).

Having lower MFT can also compensate for the thermal relations dictated by small size (May 1976; Vogt and Heinrich 1983). Lower MFTs allow individuals to engage in activities at lower ambient temperatures without the need to raise thoracic temperature above ambient. Thus, they do not need to

maintain a large differential between thoracic and ambient temperature in order to be active, and, as a result, they do not suffer the associated heat loss, which would be particularly acute in the smallest of perchers. I found *Sympetrum* spp. to have the lowest MFTs among Interior Alaska species and to have lower MFTs than comparable species at lower latitudes, except for *Sympetrum* spp. from Maine (Vogt and Heinrich 1983). For the heavier perchers, *Leucorrhinia* spp. and *Libellula quadrimaculata*, MFTs are not consistently lower than species from lower latitudes. A possible explanation for this is that during the majority of their late spring/early summer flight season, low ambient temperatures are often infrequent or of short duration, except overnight roosting temperatures. At this time both T_a and S_r are increasing toward their seasonal maxima. Thus, low MFTs may be unnecessary for these ectothermic species and could potentially restrict beneficial activity at higher ambient temperatures.

With little ability to generate heat, the smallest perchers might be expected to emerge in late spring/early summer when ambient temperature and solar radiation approach their maxima. Early summer emergence could potentially offset the effect of small mass on thermal relations. However, the least massive perchers were active during late summer, a period corresponding to the lowest solar radiation (Wendler and Eaton 1981) and ambient temperature during the flight season of any Interior Alaska dragonflies. This is likely a consequence of their obligate, univoltine phenology (Norling 1971; Corbet 1999) that may also restrict the mass they can attain in this region.

For all Interior Alaska perchers, activity significantly increased with increasing ambient temperature. In contrast, only *Sympetrum* spp. displayed a significant decrease in activity with increasing solar radiation. On a daily basis, the average number of hours of activity at ponds varied considerably. *Sympetrum* spp. were active for five to seven hours, whereas both *Leucorrhinia* spp. and *Libellula quadrimaculata* were active for 16 and 15 hours, respectively (Fig. 2.8).

Fliers

The larger dragonflies of Interior Alaska follow the general pattern of flier behavior, defending territory and pursuing mates and prey while continuously on the wing. When they perch at ponds, they tend to perch vertically on vegetation and only for short periods (Corbet 1963, 1999; May 1976, 1978, 1991; Grabow and Ruppell 1995), although some have been reported to perch horizontally on the ground and gravel in Alaska when light levels are low (Donnelly 1993). The threefold variation in flier mass is associated with a large difference in thermoregulating ability but is not associated with a significant difference in MFT. Because fliers tend to be more massive than perchers, their greater mass and relatively low surface area:volume increases thermal inertia (Cossins and Bowler 1987) and could increase thermal resistance and slow the rate of exogenous warm-up. The low surface area:volume potentially could delay the daily on-set of flight (Vogt and Heinrich 1983); however, for Interior Alaska fliers, the ability to increase thoracic temperature by wing-whirring as

well as retaining and dissipating endogenous heat appears to confer independence from environmental conditions while diminishing the need for lower MFT set points

For body masses above approximately 0.2 g, I found that the rate of passive cooling did not significantly decrease with increasing mass (Fig. 2.3) and that all Interior Alaska fliers retained heat equally well. Wing loading increased with flier mass. However, wing loading did not differ among three species, the flier *Cordulia shurtleffii* and the perchers *Leucorrhinia* spp. and *Libellula quadrimaculata*, despite significant differences in mass. This suggests that the larger of these species may have lower wing loading than expected. Thus, the flier C. *shurtleffii* may generate less heat in flight than expected for its mass. The combination of lower passive cooling rate and lower wing loading in *Cordulia shurtleffii* allows it to thermoregulate moderately well, despite evidence that although it need s relatively high T_a to initiate activity. In contrast, low passive cooling rate and high wing loading in *Aeshna* spp. allows for greater ability to thermoregulate over a wide range of ambient temperatures. As for perchers, convection appears to be the main avenue of heat loss in these fliers. However, in the case of the fliers, excess heat produced by the flight muscles is shunted to the abdomen and then dissipated through convection.

As mass increases for Interior Alaska fliers, the dependence of thoracic temperature on operative temperature decreases. With greater mass, the elevation and maintenance of thoracic temperature at low ambient temperature

as well as the ability to shunt hot hemolymph from the thorax to the abdomen at high ambient temperatures allows aeshnids to function as classic periodic endotherms (Heinrich 1974; May 1976 Bartholomew and Heinrich 1978). Once aeshnids attained MFT and arrived at a pond, their activity was independent of both T_a and S_r (Table 2.3), and they remained active at ponds for approximately 17 hours/day over their flight season. In contrast, *C. shurtleffii* shows a significant decrease in activity with increasing T_a (Table 2.1) and is active between 11-13 hours/day.

Cordulia shurtleffii appears to be constrained at both low and high temperature, and this may account for its shorter window of daily activity (Fig. 2.8). The ambient temperature required for initial *C. shurtleffii* activity was higher than for any other species in the region (Fig. 2.6), which may delay the onset of activity. On the other hand, when I captured individuals, nearly 60% of *C. shurtleffii* had T_{th} of 36° C and 33% of individual *C. shurtleffii* with T_{th} of 39° C or greater. The high thoracic temperature may be a consequence of its small mass, low passive cooling rate, and moderate thermoregulating ability to dissipate excess thoracic heat near temperatures of 40° C. Lutz and Pittman (1970) reported that in general anisoptera activity decreases near 36° C. May (1976) studied a small Florida flier, *Tramea carolina,* of comparable mass (0.15 - 0.36 g) and behavior to *C. shurtleffii. Tramea carolina* ceases flying when ambient temperatures approach 34°C and has a maximum voluntary tolerance (MVT) of approximately 38.5°C (May 1976). Ubukata (1975) speculated that

Cordulia aenea amurensis from Japan (mass not reported) decreased activity when ambient temperature approached 35°C. Therefore, the high thoracic temperatures recorded for *C. shurtleffii* are probably approaching its maximum voluntary range and may require additional heat dissipating activity.

By supplementing physiological thermoregulation with behavioral methods, *C. shurtleffii* remains active, but for fewer hours a day than all species except *Sympetrum* spp. (Fig. 2.8). Because I restricted my investigation of thermoregulation to adult activity at ponds, I only have incidental observations of perching activity in nearby fields and woods. At one pond I observed *C. shurtleffii* perched inclined on a mound of soil approximately 20 - 30 m away from the pond beginning in the late morning and continuing through early afternoon. They neither appeared to be consuming prey nor did they cant their wings downward and foreword as perchers do in order to shield the thorax; however, the slope of the mound and body of the dragonfly may have allowed it to shield its thorax without having to move its wings into the heat-dissipating posture. The similarity in general perching posture between perchers and *C. shurtleffii* may allow the latter to behaviorally dissipate heat. This, of course, needs to be verified. Some percher-like behavior has been reported for smaller fliers. For instance, May (1987) noted that the small Corduliid flier *Tetragoneuria cynosura* (0.15g) sought shade as T_a increased. This behavior remains a possible thermoregulatory method for *C. shurtleffii.*

Prior to taking-off from this percher-like position on the mound and heading back toward the pond, *C. shurtleffii* did not wing–whir, which may indicate that thoracic temperature was not allowed to reach levels low enough to require endogenous heat production to reach MFT. On a number of occasions, I did witness *C. shurtleffii* wing-whirring in the field after perching vertically in vegetation while consuming prey, although I could not elicit this behavior in the lab. The intermittent use of wing-whirring for adjustment of thoracic temperature in addition to preflight warm-up has also been documented in various species (May 1976, 1998) including the male cicada killer wasp (*Sphecius speciosus*) (Coelho 2001). Despite its moderate ability to thermoregulate, *C. shurtleffii*'s small size may not allow it to physiologically dissipate heat fast enough as ambient temperature increases. Therefore, alternating between basking and wing-whirring at high rather than low ambient temperature may offer a finer control over body temperature than endothermy or ectothermy alone (May 1976).

Having lower MFT in combination with an ability to thermoregulate would seem to be the best situation for fliers. With both of these traits, fliers could take-off at low temperature without expending energy on wing-whirring and regulate body temperature during peak T_a and S_r; however, I found that MFTs of Interior Alaska fliers do not consistently differ either among themselves or from those of lower latitude species. This supports the ideas of Vogt and Heinrich (1983) and May (1987, 1991) that in contrast to perchers, flier MFT is

not dependent on climatic conditions within their geographical range. One reason may be the near universal ability of Aeshnidae and Corduliidae to wing whir (May 1976). Wing whirring allows individuals to increase thoracic temperature to MFT without having lower MFT set points or sacrificing the ability to operate at high body temperature. One indication that wing whirring allows fliers to be active at low temperature is that aeshnids are active at ponds at approximately the same time as the smaller perchers, which rely on exogenous inputs of T_a and S_r to achieve MFT. Although *C. shurtleffii* wing-whir and have MFT set points no different than aeshnids, the T_a at which wing whirring commences may differ and constrain *C. shurtleffii* activity to more favorable environmental conditions. Since *C. shurtleffii* activity decreases with increasing temperature, it may be more advantageous for them to emerge when season climatic conditions are intermediate between their seasonal maximum and minimum. In contrast, the phenology of aeshnids appears fairly independent of season. The activity of these massive species is not highly constrained by climatic conditions and their multi-year life cycle (Norling 1971, 1984) may result in their emerging throughout the summer once they have obtained a threshold size.

Tradeoffs in Thermoregulatory Strategy between Perchers and Fliers

In many insects, elevated thoracic temperature is positively correlated with the intensity and duration of activities that directly influence fitness such as prey capture, predator avoidance, and, ultimately, reproductive success

(Heinrich 1977, Convey 1989; Marden 1992). Heinrich (1977) noted that positive selection for performance at high temperature may be inversely correlated to low temperature performance (Cossins and Bowler 1987; Hochachka and Somero 2002). Specialization at either extreme may preclude the other due to deactivation and, eventually, denaturation of flight muscle enzymes. In my examination of Interior Alaska dragonflies, I found that both the smallest and largest species were active at ambient temperatures of approximately 14° C. This is notable because they have strikingly different abilities to elevate and maintain thoracic temperature (Table 2.1). The thermoconforming *Sympetrum* spp. have a low MFT set point that allows activity to commence when little behavioral thoracic warming is possible. Although they can elevate body temperature, they are unable to thermoregulate. To have both a lower MFT and an ability to thermoregulate may be energetically too costly; therefore, for small species in cooler climates, ectothermy and lower MFT may save energy by allowing species to be active without having to maintain an elevated T_{th}. Once environmental conditions reach MFT set points, the thoracic temperature of *Sympetrum* spp. remains elevated by behavioral repositioning. This can be accomplished at minimal cost to these strict ectotherms due to their low thermal resistance. If these species are cold adapted, their muscle enzymes may be susceptible to decreased function at high temperature. This fits my finding that the thermal niche of *Sympetrum* spp. is highly constrained by diurnal patterns in T_a and S_r

as well as the seasonal flux in these variables. In contrast, MFT for the aeshnids is approximately 20°C, 6°C higher than that of *Sympetrum* spp. Aeshnids appear to employ the physiological mechanism of wing-whiring to raise thoracic temperature to MFT; this enables them to be active at lower ambient temperatures, despite having a higher MFT. This may also allow specialization of muscle enzymes for high temperature performance.

The least massive flier, *C. shurtleffii,* and the most massive percher, *Libellula quadrimaculata,* share many thermoregulatory characteristics with the aeshnids. Although these two species are significantly smaller than the aeshnids, their passive cooling rates and MFTs do not significantly differ from those of the aeshnids; however, *C. shurtleffii* and *Libellula quadrimaculata* are not active at low ambient temperatures. One reason for this in *Libellula quadrimaculata* may be an inability to wing whirr, as Heinrich and Casey (1978) have noted for another *Libellula* species. Therefore, *Libellula quadrimaculata* may remain perched until ambient conditions increase and passively heat flight muscles to MFT, delaying the onset of flight. This circumstance has been reported for many perchers (Vogt and Heinrich 1983). Explaining the delay in activity for *C. shurtleffii* is more problematic. There appear to be two possible explanations for my findings. First, although I have noted that this species can wing whir after consuming prey during the day, it remains to be shown whether it can endothermcially increase thoracic temperature at other times. Second, Vogt and Heinrich (1983) have noted that for some species the voluntary

takeoff temperature is substantially higher than MFT. They speculated that these species may remain perched until they reach thoracic temperatures high enough for fast, agile flight; this would allow for increased maneuverability for catching prey and avoiding predators. Hence, *C. shurtleffii* may delay the onset of flight even after achieving MFT.

Leucorrhinia spp. appear to employ aspects of both MFT and thermoregulating strategies. Although the mass of *Leucorrhinia* spp. is statistically greater than *Sympetrum* spp., passive cooling rate is not. The moderate thermoregulating ability of *Leucorrhinia* spp. is similar to larger perchers and fliers. It may be that in the range of mass between *Sympetrum* spp. and *Leucorrhinia* spp. both thermal conformity and thermoregulation are viable strategies. The transition from thermoconformity in *Sympetrum* spp. to thermoregulation in *Leucorrhinia* spp. may be governed by the difference in wing loading as well as the difference in environmental conditions during each species' flight season. In *Leucorrhinia* spp., higher wing loading potentially generates enough heat as a byproduct of flight to favor thermoregulation while the ability to elevate body temperature may also diminish the need for very low MFT. Finally, warmer summer and cooler early fall conditions may favor thermoregulation in *Leucorrhinia* spp. and thermoconformity in *Sympetrum* spp.

My findings on MFTs and thermoregulating ability among Interior Alaska dragonflies largely confirm the major results of May (1976), Heinrich and Casey (1978), and Vogt and Heinrich (1983). I show that MFTs of perchers do not

decrease at higher latitudes or in cooler climates when compared to the lowest MFTs recorded for similar species from Maine. This suggests that there may be a lower limit on MFT set points in dragonflies. Like MFT, thermoregulating ability increases with increasing mass among perchers and fliers; however, for small species with low thermal inertia, low MFT and thermoconformity may be favored in cooler climates and during colder seasonal periods (but see May 1998). Finally, my results suggest a tradeoff between MFT and thermoregulating ability such that the ability to maintain thoracic temperature may decrease the need for lower MFT; however, when flight season is late summer/early fall when the major ectothermic sources are in decline at higher latitudes, a lower MFT may be more important than is the ability to maintain a thoracic temperature over a wide range of ambient temperatures especially in smaller species.

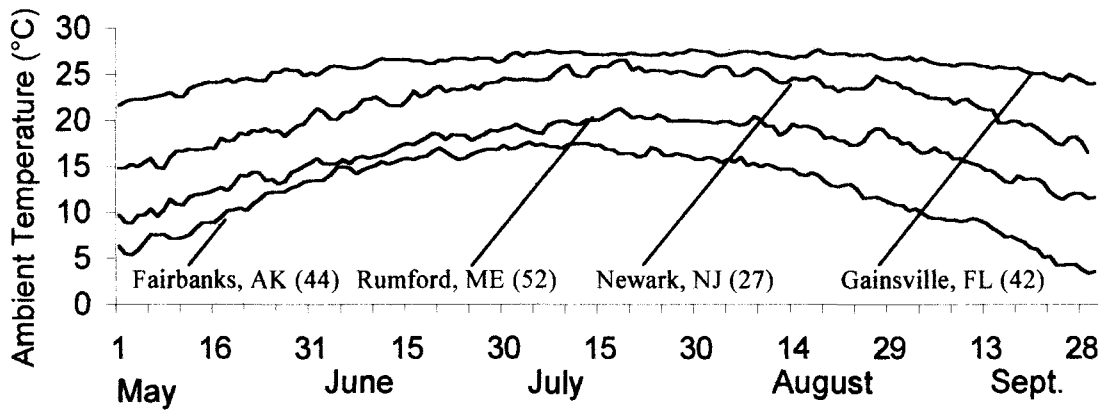

Figure 2.1. Mean daily temperature derived from daily maximum and minimum temperatures from localities where MFT of dragonflies have been studied. Number next to each locality is years of data.

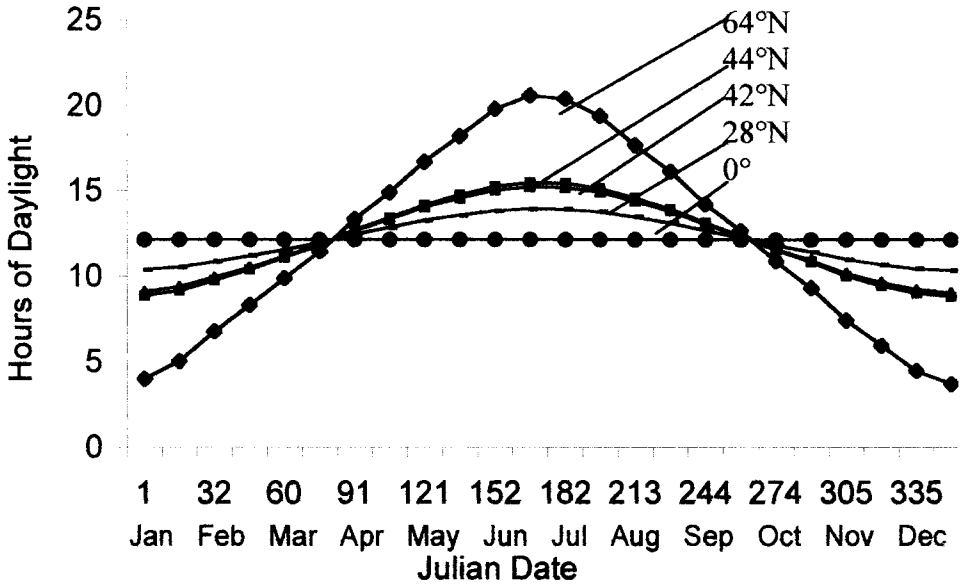

Figure 2.2. Hours of daylight as a function of Julian day and latitude.

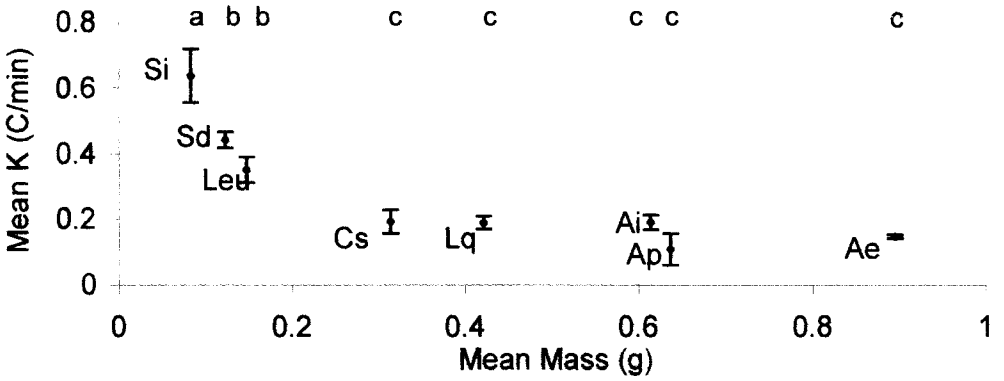

Figure 2.3. Mean (±SE) passive cooling as a function of mean (±SE) total body mass. Different letters above bars indicate significant differences in means ($p < 0.05$; LS Means with Tukey-Kramer precedure for multiple comparisons). Abbreviations beside bars are as follows: Aesh = *Aeshna* spp., Ae = *A. eremita*, Ai = *Aeshna interrupta*, Ap = *A. palmata*, Cs = *Cordulia shurtleffii*, Lq = *Libellula quadrimaculata*, Leu = *Leucorrhinia* spp., Sd = *Sympetrum danae*, Si = *S. internum*.

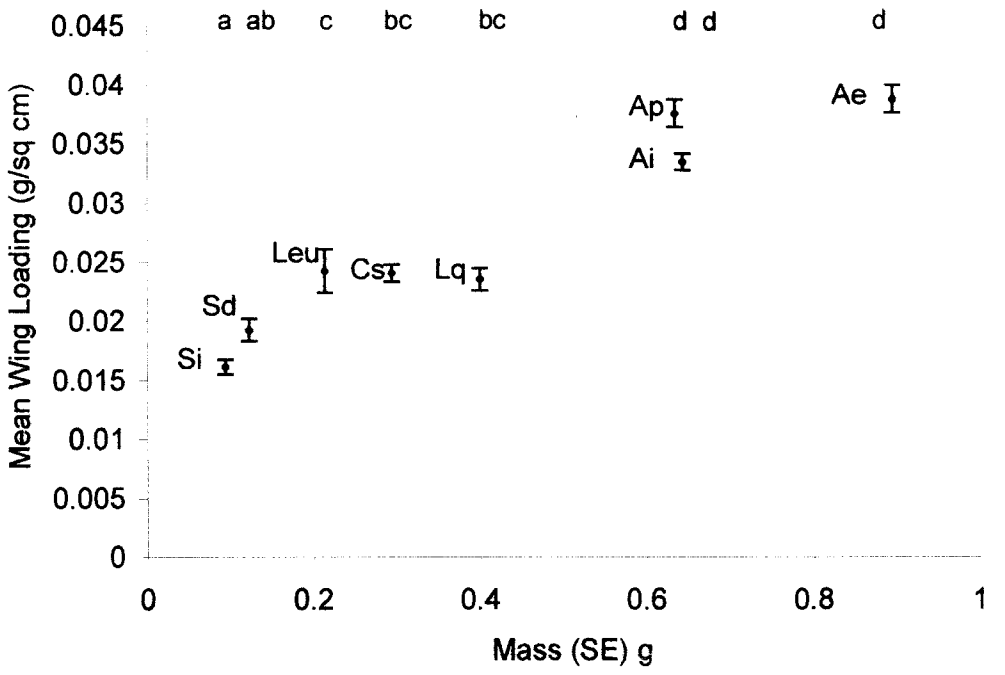

Figure 2.4. Mean (±SE) wing loading as a function of total body mass. For abbreviations, see fig. 3. Different letters above bars indicate significant differences in means ($p < 0.05$; LS Means with Tukey-Kramer procedure for multiple comparisons).

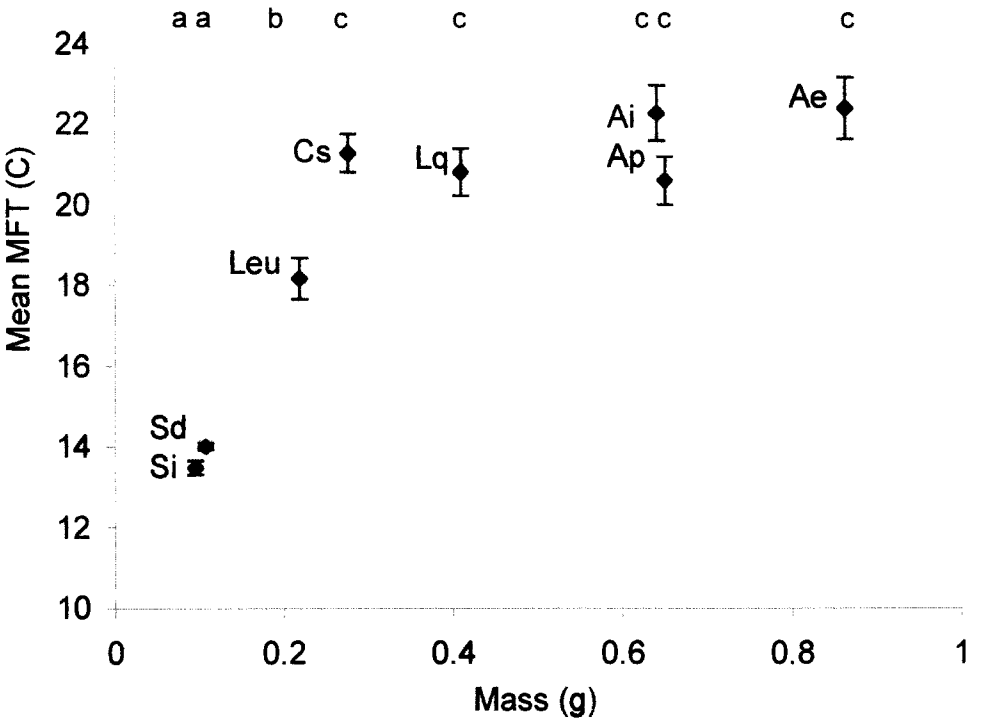

Figure 2.5. Dependence of mean minimum flight temperature as a function of mean total body mass. Letters above bars indicate no difference ($p > 0.05$) in means (LS Means with Tukey-Kramer procedure for multiple comparisons). For abbreviations and behavior, see fig. 2.3.

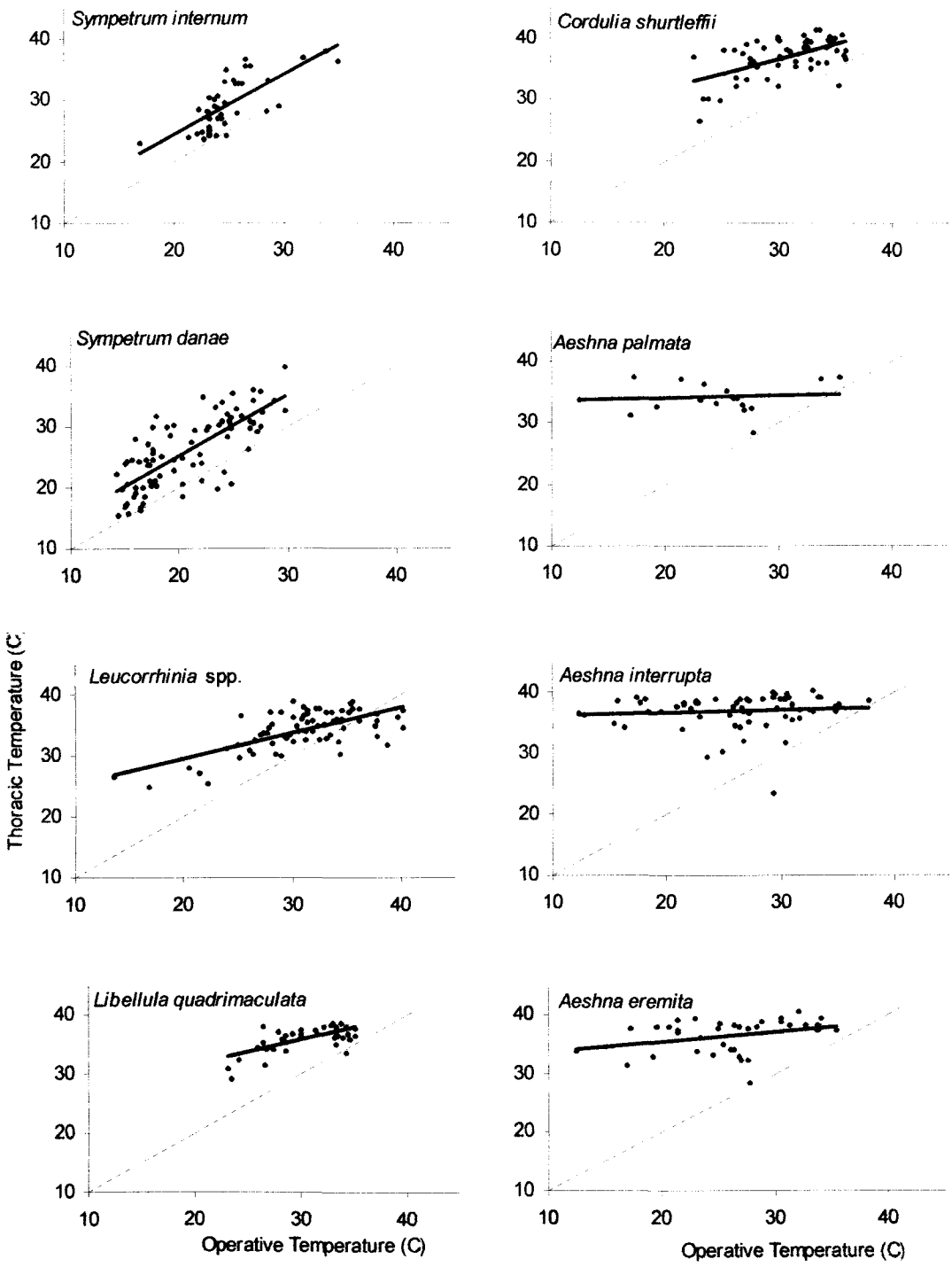

Figure 2.6. The relationship between T_{th} and T_e for each species. TPI is computed as the slope (solid line) of the simple linear regression of T_{th} on T_e. To determine if a species thermoregulates, I compare its TPI value to the theoretical, isothermal line (dotted line where slope = 1) that represents perfect thermal conformity.

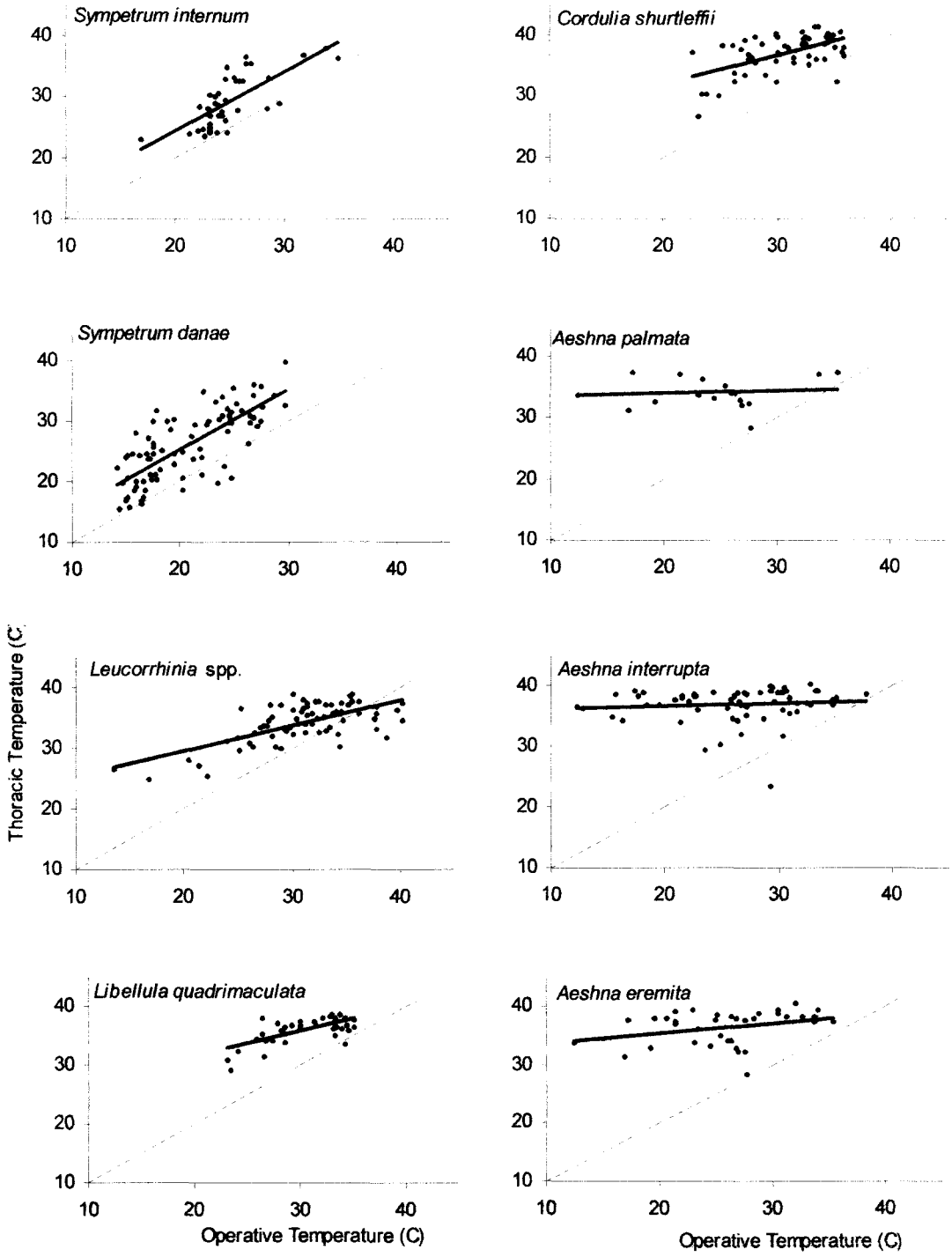

Figure 2.6. The relationship between T_{th} and T_e for each species. TPI is computed as the slope (solid line) of the simple linear regression of T_{th} on T_e. To determine if a species thermoregulates, I compare its TPI value to the theoretical, isothermal line (dotted line where slope = 1) that represents perfect thermal conformity.

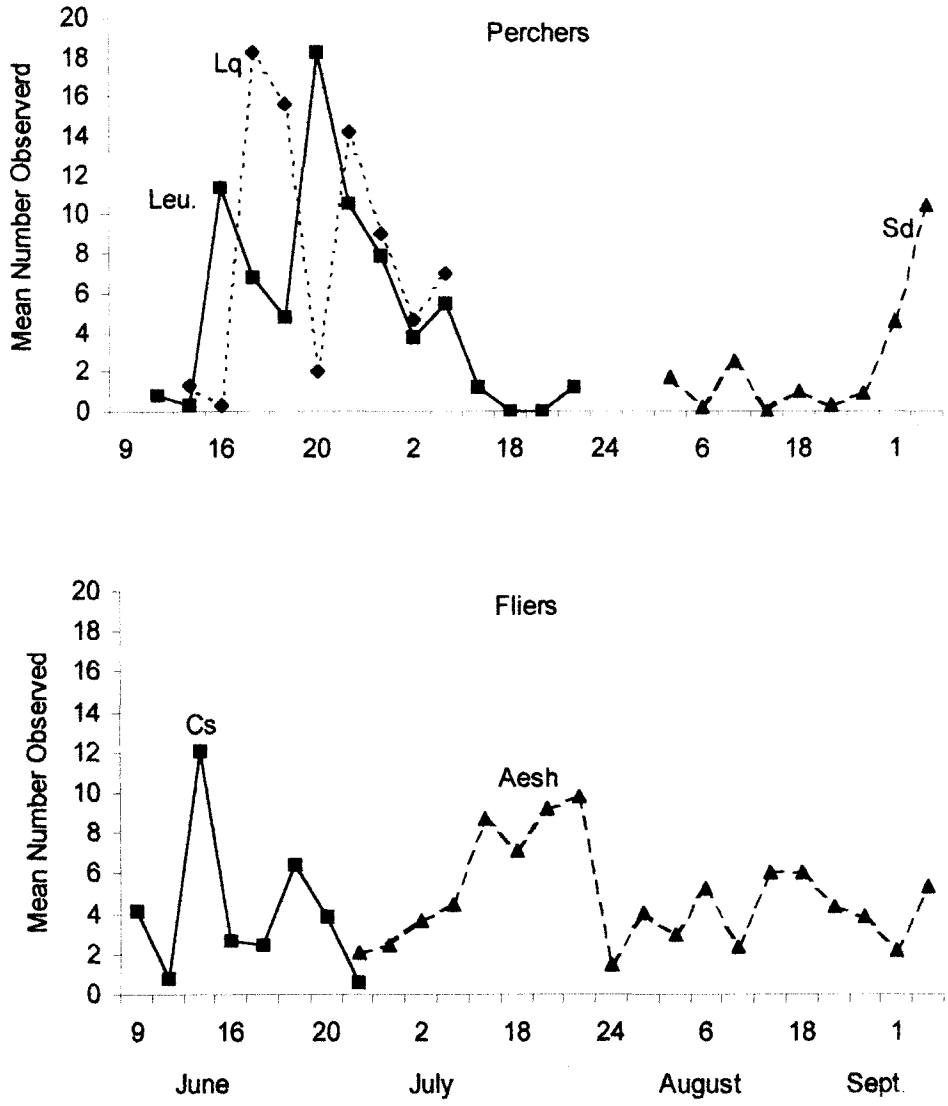

Figure 2.7. Phenology of adult odonates (Anisoptera) from interior Alaska, 2001. The measure of activity is the mean number of odonates found in 12 eight m^2 quadrates at the beginning of each hourly survey period divided by the number of survey periods per day. For abbreviations, see fig. 3.

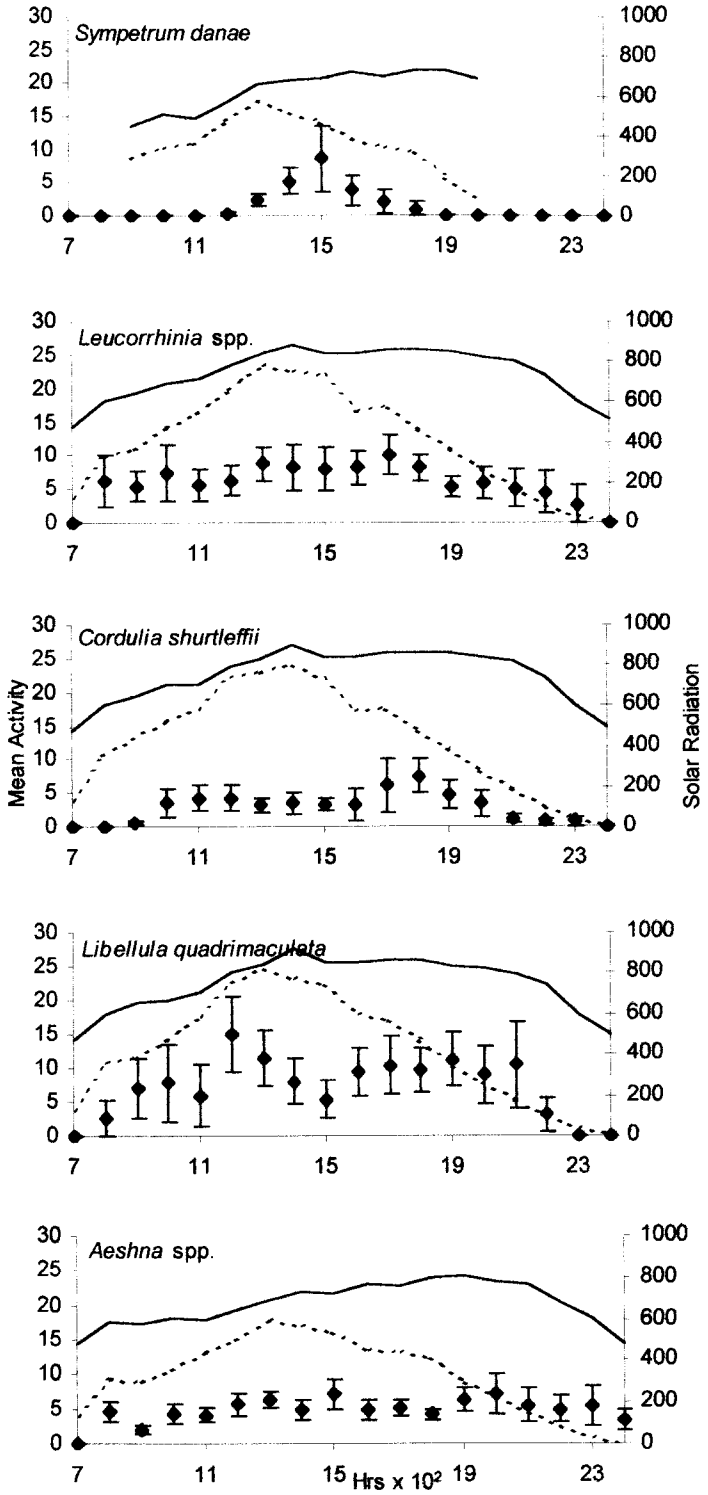

Figure 2.8. Mean (±SE) activity, ambient temperature, and solar radiation over an entire flight season. Top, solid line represents mean ambient temperature (°C) and bottom, dotted line represents mean solar radiation (Watts-m^2) from pre- and post- survey counts.

Table 2.1. Predominate behavior at ponds, mass, and thermoregulatory data for dragonfly species of Interior Alaska arranged from least to most massive. Morphometric data were collected in (2000-2001).

Taxon	Behavior	Mean body Mass (g) [+] (SE) *N*	Mean thoracic Mass (g) [+] (SE) *N*	Thermoregulatory performance Index (SE) *N*
Sympetrum internum	Percher	0.09[a] (0.002) 55	0.04[a] (0.003) 13	0.96[*] (0.14) 39
Sympetrum danae	Percher	0.10[a] (0.001) 139	0.05[a] (0.007) 20	0.98[*] (0.09) 82
Leucorrhinia hudsonica, L. borealis, L. proxima	Percher	0.21[b] (0.005) 106	0.09[a] (0.005) 35	0.40 (0.05) 73
Cordulia shurtleffii	Flier	0.27[c] (0.004) 46	0.11[b] (0.003) 19	0.46 (0.09) 55
Libellula quadrimaculata	Percher	0.40[d] (0.006) 85	0.19[c] (0.004) 31	0.47 (0.05) 44
Aeshna palmata	Flier	0.64[e] (0.004) 149	0.25[d] (0.003) 63	0.1[**] (0.08) 30
Aeshna interrupta	Flier	0.65[e] (0.004) 106	0.27[e] (0.004) 38	0.06[**] (0.03) 58
Aeshna eremita	Flier	0.86[f] (0.009) 47	0.36[f] (0.005) 25	0.17[**] (0.08) 36

[+] Different superscript letters indicate a significant difference in means (LS Means with Tukey-Kramer adjustment for multiple comparisons)

[*] TPI does not differ from a value of 1-- thermoconformer

[**] TPI does not differ from a value of 0-- thermoregulator

Table 2.2. Minimum flight temperature comparisons between Interior Alaska species and lower latitude species from previous studies.

Interior Alaska Taxon	Mean Mass (g)	*n***	Mean MFT (SE)	Lower Latitude Taxon	Be*	Mean Mass (g)	*n***	Mean MFT (SE)	*t*	*P*
Sympetrum internum	0.09	4	13.47 (0.17)	*Sympetrum vicinum*[1]	p	0.1	10	15.4 (.22)	17.52	< 0.001
"				*Sympetrum obtrusum*[2]	p	0.13	5	13.2 (.1)	-2.81	0.05
"				*Sympetrum vicinum*[2]	p	0.14	10	12.5 (.1)	-7.39	0.003
Sympetrum danae	0.10	25	14.00 (0.09)	*Sympetrum vicinum*[1]	p	0.1	10	15.4 (.22)	19.36	< 0.001
"				*Sympetrum obtrusum*[2]	p	0.13	5	13.2 (.1)	-16.59	< 0.001
"				*Sympetrum vicinum*[2]	p	0.14	10	12.5 (.1)	14.76	< 0.001
Leucorrhinia spp.	0.21	13	18.16 (0.51)	*Pachydiplax longipennis*[3]	p	0.17	41	20.9 (.29)	12.7	< 0.001
"				*Erythemis simplicicollis*[3]	p	0.27	30	19.7 (.36)	7.64	< 0.001
Cordulia shurtleffii	0.27	6	21.27 (0.47)	*Tramea carolina*[3]	f	0.38	20	20.75 (.44)	-2.4	ns
Libellula quadrimaculata	0.40	19	20.79 (0.58)	*Libellula spp.*[3]	p	0.45	29	19.5 (.25)	-9.11	< 0.001
Aeshna interrupta	0.64	6	20.58 (0.68)	*Gynacantha nervosa*[3]	f	0.63	3	21 (.35)	1.31	ns
Aeshna palmata	0.65	9	22.25 (0.60)	*Gynacantha nervosa*[3]	f	0.63	3	21 (.35)	-4.07	0.025
Aeshna eremita	0.86	6	22.38 (0.76)	*Gynacantha nervosa*[3]	f	0.63	3	21 (.35)	-3.7	0.01
"				*Anax junius*[3]	f	1.04	4	25 (1.2)	3.67	ns

*Be= behavior--p = percher; f = flier
**n = number tested for MFT
[1] May 1998 -- Data from New Jersey
[2] Vogt and Heinrich 1983 -- Data from Maine
[3] May 1976 -- Data from Florida

Table 2.3. Results of linear mixed model analysis of dragonfly activity.

Taxon	Source	Estimate	SE	df	*F*	*P*
Sympetrum danae	Time	-2.450	3.144	1, 52	0.61	Ns
	Ta	6.9790	1.975	1, 52	12.48	0.0009
	Sr	-0.084	0.029	1, 52	8.31	0.0057
	$Time^2$	0.3426	0.147	1, 52	5.43	0.0237
	Time x Ta	-0.5082	0.125	1, 52	16.37	< 0.0001
	Time x Sr	0.0113	0.002	1, 52	18.7	< 0.0001
	Ta x Sr	-0.0028	0001	1, 52	4.63	0.036
Leucorrhinia spp.	Time	-5.2562	1.468	1, 120	12.82	0.0005
	Ta	1.1543	0.236	1, 120	23.88	< 0.0001
	Sr	0.0066	0.004	1, 120	2.72	ns
	$Time^2$	0.1635	0.047	1, 120	11.87	0.0008
Cordulia shurtleffii	Time	6.6614	1.290	1, 91	26.67	< 0.0001
	Ta	-0.5901	0.183	1, 91	10.35	0.0018
	Sr	-0.0049	0.003	1, 91	1.75	ns
	$Time^2$	-0.2115	0.042	1, 91	24.57	< 0.0001
Libellula quadrimaculata	Time	-5.415	2.119	1, 86	6.53	0.0124
	Ta	1.8473	0.302	1, 86	37.13	0.0001
	Sr	0.0024	0.006	1, 86	0.14	ns
	$Time^2$	0.1553	0070	1, 86	4.9	0.0295
Aeshna spp.	Time	0.1238	0.1089	1, 149	1.29	ns
	Ta	0.1258	0.1252	1, 149	1.01	ns
	Sr	0.0017	0.002	1, 149	0.51	ns

Literature Cited

Bakken, G.S. 1976. A heat transfer analysis of animals: unifying concepts and the applications of metabolism chamber data to field ecology. J. Theor. Bio. 60: 337-384.

--. 1980. The use of standard operative temperature in the study of the thermal energetics of birds. Physio. Zool. 53: 108-119.

--. 1992. Measurement and application of operative and standard operative temperatures in ecology. Am. Zool. 32:194-216.

Bakken, G.S., Gates, D.M. 1975. Heat-transfer analysis in animals: some implications for field ecology, physiology, and evolution. Pages 255-90 in DM Gates and RB Schmerl, eds. Perspectives of Biophysical Ecology. Berlin: Springer.

Bartholomew, G.A., Heinrich, B. 1978. Endothermy in African dung beetles during flight, ball making, and ball rolling. J. Exp. Bio. 73:65-83.

Berthold, A.A. 1835. Neue Versuche uber die Temperatur der kaltblutigen Thiere. Gottingen, in der Dieterischen Buchhandlung

Bishop, J.A., and Armbruster, W.S. 1999. Thermoregulatory ability of Alaskan bees: effects of size, phylogeny and ecology. Func. Ecol. 13:711-24.

Casey, T.M. 1992. Biophysical ecology and heat-exchange in insects. Am. Zool. 32:225-237.

Church, N.S. 1959. Heat loss and the body temperatures of flying insects II. Heat conduction within the body and its loss by radiation and convection. J. Exp. Bio. 37: 186-212.

Convey, P. 1989. Influences on the choice between territorial and satellite behavior in male *Libellula quadrimaculata* Linn. (Odonata: Libellulidae) Behaviour 109:125-141.

Corbet, P.S. 1963. A biology of dragonflies. Quadrangle Press, Chicago.

Corbet, P.S. 1999. Dragonflies: behavior and ecology of odonata. Cornell University Press, New York.

Corbet, S.A., M. Fussell, R. Ake, A. Fraser, C. Gunson, A. Savage, and K. Smith. 1993. Temperature and the pollinating activities of social insects. Ecol. Entom. 18:17-30.

Cossins, A.R., and K. Bowler. 1987. Temperature Biology of Animals Chapman and Hall: New York.

Cowles, R.B., and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Am. Mus. Nat. Hist. 83:265-296.

Crawford, K.M., J.R. Spotila, and E.A. Standora. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology 64:989-999.

Donnelly, N. 1993. Collecting in Alaska- or- Nanick of the North. Agria 5:11-12.

Dreisig, H. 1980. Daily activity, thermoregulation, and water loss in the tiger beetle *Cicindela hybrida*. Oecologia 44:376-89.

--. 1984. Control of body temperature in shuttling ectotherms. J.Thermal Biol. 9:229-233.

--. 1985. A time budget model of thermoregulation in shuttling ectotherms. J. Arid Environ. 8:191-205.

--. 1990. Thermoregulatory stilting in tiger beetles, *Cicindela hybrida* L. J. Arid Environ. 19:297-302.

--. 1995. Thermoregulation and flight activity in territorial male graylings, *Hipparchia semele* (Satyridae), and large skippers, *Ochlodes venata* (Hesperiidae). Oecologia 161:169-176.

Forrester, N.D., F. Guthery, S.D. Kopp, and W.E. Cohen. 1998. Operative temperature reduces habitat space for Northern Bobwhites. J. Wild Manage. 62:1506-11.

Grabow, K., and G. Ruppell. 1995. Wing loading in relation to size and flight characteristics of Europena Odonata. Odonatologica 24:175-186.

Heath, J.E. 1964. Reptilian thermoregulation: evaluation of field studies. Science 146:784-85.

Heath, J.E. 1967. Temperature responses of the "17-year" cicada, *Magicicada cassinii.* Am. Midland Natural. 77:64-76.

Heath, J.E., and P.A. Adams. 1965. Temperature regulation in the sphinx moth during flight. Nature 205:309-310.

Heinrich, B. 1974. Thermoregulation in endothermic insects. Science 185:747-756.

--. 1977. Why have some animals evolved to regulate a high body temperature? Am. Nat. 111: 623-640.

--. 1981. Ecological and evolutionary perspectives. Pages 235-302 in B. Heinrich, ed. Insect Thermoregulation. Wiley, New York.

--. 1993. The Hot-Blooded Insects: strategies and mechanism of thermoregulation. Harvard University Press: Cambridge.

Heinrich, B., and T.M. Casey. 1978. Heat transfer in dragonflies: "Fliers" and "Perchers". J. Exper. Biol. 74:17-36.

Heinrich, B., and T.P. Mommsen. 1985. Flight of winter moths near 0°C. Science 228:177-179.

Hertz, P.E., R.B. Huey, and R.D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am. Nat. 142:796-818.

Hochschka, P.W., and G.N. Somero. 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, Oxford.

Lutz, P.E. and A.R. Pittman. 1970. Some ecological factors influencing a community of adult odonata. Ecology 51:279-285.

Marden, J.H. 1989. Bodybuilding dragonflies: costs and benefits of maximizing flight muscle. Physio. Zool. 62:505-521.

Marden, J.H., M.G. Kramer, and J.H Frisch. 1996. Age-related variation in body temperature, thermoregulation and activity in a thermally polymorphic dragonfly. J. Exper. Biol. 199:529-535.

May, M. L. 1976. Thermoregualtion and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecol. Monogr. 46:1-32.

--. 1978. Thermal adaptations of dragonflies. Odonatologica 7:27-47.

--. 1987. Body temperature regulation and responses to temperature by male *Tetragoneuria cynosura* (Anisoptera: Corduliidae). Adv. Odonatol. 3:103-119.

--. 1991. Thermal adaptations of dragonflies, revisited. Advan. Odonatol. 5:71-88.

--. 1995. Dependence of flight behavior and heat production on air temperature in the green darner dragonfly *Anax junius* (Odonata: Aeshnidae). J. Exp. Biol. 198:2385-2392.

--. 1998. Body Temperature regulation in a late-season dragonfly, *Sympetrum vicinum* (Odonata: Libellulidae). Inter. J. Odonatol. 1:1-13.

Michiels, N.K, and A.A. Dhondt. 1987. Coexistence of three *Sympetrum* species at Den Diel, Mol, Belgium (Anisoptera: Libellulidae) Odonatologica 16: 347-360.

Newport, G. 1837. On the temperature of insects, and its connection with the functions of respiration and circulation in the class of invertebrated

animals. Philosophical Transactions of the Royal Society, London 127: 259-339.

Norling, U. 1971. The life history and seasonal regulation of Aeshna viridus Eversm. in southern Sweded (Odonata) Entom. Scandanavia 2:170-190.

Norling, U. 1984. Life history patterns in the northern expansion of dragonflies. Advan. Odonatol. 2:127-156.

O'Neill K.M., and W.P. Kemp. 1990. Behavioral responses of the Robber Fly *Stenopogon inquinatus* (Diptera: Asilidae) to variation in the thermal environment. Environ. Entom. 19:459-464.

O'Neill K.M., and W.P. Kemp. 1992. Behavioral thermoregulation in two species of robber flies occupying different grassland microhabitats. J. Thermal Biol. 17:323-331.

Parker, M.A. 1982. Thermoregulation by diurnal movement in the barberpole grasshopper (*Dactylotum bicolor*). Am. Midl. Nat. 107: 228-237.

Polcyn, D.M. 1994. Thermoregualtion during summer activity in Mojave Desert dragonflies (Odonata: Anisoptera) Funct. Ecol. 8:441-449.

Sailor, R.I. 1950. A thermophobic insect. Science 112: 743.

Schultz, T.D. 1998. The utilization of patchy thermal microhabitats by the ectothermic insect predator, *Cicindela sexguttata*. Ecol. Entom. 23:444-450.

Seebacher, F., G.C. Grigg, and L.A. Beard. 1999. Crocodiles as dinosaurs: behavioral thermoregulation in very large ectotherms leads to high and stable body temperatures. J. Exp. Biol. 202:77-86.

Seebacher, F. 2000. Heat transfer in a microvascular network: the effect of heart rate on heating and cooling in reptiles (*Pogona barbata* and *Varanus varius*). J. Theor. Biol. 203:97-109.

Singer, F.D. 1987. The behavioral and physiological ecology of dragonflies, PhD Dissertation U of Minnesota.

Tracy, C.R. 1977. Minimum size of mammalian homeotherms: role of the thermal environments. Science 198:1034-35.

Turner, J., J.R. Henschel, and Y.D Lubin. 1993. Thermal constraints on prey-capture behavior of a burrowing spider in a hot environment. Behav. Eco. Sociobiol. 33:35-43.

Ubukata, H. 1973. Life history and behavior of a corduliid dragonfly, *Cordulia aenea amurensis* Selys. I. Emergence and Pre-reproductive periods. J.Faculty Science Hokkaido University. Series VI: 19:251-269.

Vogt, F.D., and B. Heinrich. 1983. Throacic temperature variation in the onset of flight in dragonflies (Odonata: Anisoptera) Physio. Zool. 56:236-241.

Wendler, G., and F. Eaton. 1983. Solar radiation data for Fairbanks. Geophysical Institute, University of Alaska Fairbanks.

Willmer, P.G. 1982. Microclimate and the environmental physiology of insects. Pages 1-57in M.J. Berridge, J.E. Treherne, and V.B. Wigglesworth eds. Advances in Insects Physiology, Vol. 16. Academic Press, London.

Winslow, C.E.A, L.P Herrington, and A.P Gagge. 1937. Physiological reactions of the human body to varying environmental temperatures. Amer. J.Physio. 120:1-22.

Ybarrondo, B.A., and B. Heinrich. 1996. Thermoregulation and the response to competion in the African dung beetle *Kheper nigroaeneus* (Coleoptera: Scarabaeidae). Physio. Zool. 69:35-48.